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AXIAL SUSCEPTIBILITY GRADIENTS IN ALGAE

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Introduction

Before presenting the data which constitute the subject of this paper, it is necessary to make clear the reasons which determined this venture into the botanical field and the presentation of these data to botanists for consideration and criticism. My experimental studies on the lower animals, extending over a period of years, have led me to certain conclusions concerning the nature of the physiological axes of organisms and of physiological individuality, which suggest that the physiological individual as an expression of a dynamic unity and order in protoplasm is fundamentally similar in its origin and nature in both animals and plants. The observations recorded in this paper constitute the first step in an attempt to determine whether and to what extent this is true. In order to make clear the point of view from which the investigation was undertaken, a brief statement of certain results of my experiments with animals and of the general conception toward which they point is essential.

I have shown that various lines of evidence point to the existence of a gradient in the rate of metabolism or of certain fundamental metabolic reactions as a characteristic feature of at least the chief physiological axes, and probably of all such axes in animals. Such a gradient is the earliest demonstrable indication of the axis, and in many forms persists without essential change throughout

the life of the individual, while in others it undergoes modification during the course of development. In the axial metabolic gradient of the chief axis the region of highest rate of reaction becomes the apical region or head of the individual, and in other axes the development of organs shows a definite relation to the direction of the gradient.

In the final analysis such a gradient is not self-determined by some sort of organization, but arises as the result of the differential action of factors external to the protoplasm, cell, or cell mass acted upon. If, for example, an undifferentiated cell or cell mass is stimulated at some point by the action of a factor external to it, the resulting increase in metabolic activity is not limited to the region immediately affected, but a wave of change spreads or is transmitted over or through the protoplasm with decreasing energy, intensity, or physiological effectiveness, until, if the mass be large enough, it becomes inappreciable at a greater or less distance from the point of origin. It may be likened to a wave in water or in air spreading from the point of disturbance.

This is the simplest form of metabolic gradient, but while it produces temporary changes in the protoplasm, they are usually evanescent or the lasting effect is inappreciable. If, however, the stimulation be sufficiently often repeated or sufficiently long continued at the same point, more or less persistent changes in the protoplasm may occur, which appear as differences in its capacity to react. In such a case we say that the irritability of the protoplasm is altered. Since such changes are in general proportional to the energy or intensity of the transmitted change which produces them, they must differ at different distances from the point of action of the external factor, and the result is what we may call an irritability gradient, a gradient in the rapidity, capacity, or intensity of reaction of the protoplasm. Such a gradient is, I believe, the simplest form of persistent organic or physiological axis. In the chief gradient or axis, which is that first established, the region of highest metabolic rate or highest irritability becomes the apical region, and in the more highly differentiated animals the head, or more specifically the cephalic part of the central nervous system, develops from it.

In such a metabolic or irritability gradient it is evident that the region of highest rate of reaction must control or dominate other regions within a certain range, simply because the changes transmitted from it possess greater energy or physiological effectiveness than those from other regions, and therefore constitute the chief factor in determining the general metabolic rate in these other regions within the range of its action. In plants the dominance of the apical region over other levels of the axis is a familiar fact, and I have shown that in at least the simpler animals similar relations exist along the main axis, the region of highest metabolic rate being the dominant region.

This relation of dominance and subordination dependent upon a gradient in metabolic rate or in the irritability of the protoplasm is, as I believe, the simplest kind of physiological[1] unity and order in living protoplasm, these transmitted changes are the fundamental form of physiological correlation, and the physiological individual as an expression of dynamic unity and order consists fundamentally of one or more such metabolic gradients.

According to this conception, the individual originates as one or more quantitative gradients in the dynamic processes characteristic of the specific protoplasm concerned. Morphogenesis and differentiation result from the quantitative differences existing at different levels of the gradient because the substances which remain as constituents of or inclosures in the protoplasm differ not only in amount but in kind according to the rate or intensity of metabolic activity. In this way qualitative differences arise from quantitative, and what we call differentiation results. This conception of differentiation is supported by the fact that it is possible experimentally to alter widely the character of morphogenesis by means of conditions which act primarily in a quantitative way.

If this view be correct, the physiological axiate individual is fundamentally a unity resulting from transmitted dynamic changes,

[1] The word "physiological" is used here by way of distinction. Other kinds of individuality, of unity and order in aggregates, exist in the world and some of them undoubtedly exist in organisms, but by physiological unity and order is meant that kind which seems to be peculiarly characteristic of living things, and which determines orderly space and time relations with respect to an axis; in short, an orderly form and an orderly course of development.

rather than, as often assumed, from the transportation of specific chemical substances. In other words, physiological correlation is fundamentally transmissive rather than transportative in character, and transportative correlation arises only secondarily as the result of the quantitative and qualitative differences associated with the transmitted changes. It is evident that the existence of orderly transportative correlation demands the existence of differences of some sort arranged in an orderly way, and it is this fundamental order from which the other orderly phenomena in the life of the organism result, that this theory of the individual attempts to account for.

It is not necessary to assume, however, that every individual arises in the manner described above. When an axial gradient is once established in a cell or cell mass, it may persist through division or other forms of reproduction, so that each axis of the offspring is simply the axis of the parent or a fraction of it. In such cases the processes of rejuvenescence associated with reproduction bring the different fractions to essentially the same physiological condition, that is, the fraction which represents the lower levels of the parent gradient is brought up to the same metabolic rate or rates as that representing the higher levels. Nevertheless, we must, I believe, go back to a differential action of factors external to the protoplasm concerned for the origin of the metabolic gradient and so of the axis or polarity of which it is the simplest form.

Since the energy or effectiveness of a transmitted change in protoplasm decreases with increasing distance from the point of origin, the length of a metabolic gradient, and therefore the range of dominance of the region of highest rate, is limited, the limit varying with rate or intensity of metabolic activity, irritability and conductivity of the protoplasm, etc. This limit represents the maximum size which the physiological individual can attain and remain entirely an individual under the conditions which determine the limit. If, in consequence of continued growth, of decrease in the metabolic activity of the dominant apical region, of decrease in the conductivity of the protoplasm, any part previously within the range of dominance, that is, within the limit of length of the metabolic gradient, comes to lie beyond this limit, it becomes

physiologically isolated, and if the irritability gradient in its protoplasm resulting from its former relations to the gradient persists, or if a new gradient arises in it, the reproduction of a new individual occurs. The space relations in the formation, inhibition, or development of buds in plants and the dominance of the chief growing tip seem to be fundamentally of this character. Growth in size of the plant or removal or inhibition of the chief growing tip results in physiological isolation of other parts, and new buds arise or buds previously inhibited develop.

This in brief is the conception of physiological individuality which has developed from my experimental work on the lower animals.[2] Since I have found metabolic gradients as characteristic features of the axes in animals and have been able to control and modify to a high degree size, development, and reproduction by controlling and modifying these gradients, it seemed desirable to determine whether the existence of similar gradients could be demonstrated in the simpler plants. The behavior in growth and development of the axis of the higher plant is a practical demonstration of the presence of a metabolic gradient with the apical region as the region of highest rate, but I thought it of interest to apply to some of the simple plants methods which I had used for the simple animals.

Methods and material

In the course of experimentation on the lower animals, I have found that certain relations exist between metabolic condition and susceptibility to at least many agents and conditions which interfere with, depress, or inhibit metabolism in some way. These relations are briefly as follows: To agents and conditions which affect the organism in sufficient degree to bring about death in a short time without permitting adaptation or acclimation, susceptibility varies directly with metabolic rate or with the rate of certain fundamental metabolic reactions, probably primarily the oxidations. The higher the rate of reaction the sooner death occurs, and vice versa. To agents and conditions which affect the organism to so slight a degree that more or less adaptation or acclimation is

[2] For more extended consideration of the subject see: CHILD, C. M., 1–4, 6, 7, 9–11 (chapter ix), 12.

possible, the rapidity and degree of acclimation varies under most conditions directly with the rate of metabolism; consequently in the long run the susceptibility varies inversely as the metabolic rate. Within certain limits under these conditions, the higher the metabolic rate the longer life continues, because the higher the rate, the more rapid and complete the acclimation. Thus with the same differences in metabolic rate, the relative susceptibilities to high concentrations of a given agent are the inverse of those to very low concentrations of the same agent.

These relations have been demonstrated for the cyanides, ethyl alcohol, ether and various other narcotics, acids and in marine forms for alkalies also, as well as for certain other substances and conditions, such as lack of oxygen, presence of carbon dioxide or other metabolic products in the medium, etc. It cannot be supposed that all these agents and conditions act on living protoplasm in the same way, but it is true that they all interfere with the activities of living protoplasm in some way. The general relation between susceptibility and metabolic rate is undoubtedly independent, at least to a large extent, of the particular method of action of a particular agent or condition. With a certain rate of chemical reaction in protoplasm, certain conditions as regards enzymes, aggregation of colloids, permeability, etc., are in general correlated. The chemical reactions may be retarded or inhibited by means of changes in these various protoplasmic conditions, as well as by a direct chemical action; and since all these different factors in the activity of the protoplasm are correlated, its susceptibility to at least many, if not all inhibiting agents and conditions the effect of which is not instantaneous but progressive, must vary in general with its metabolic activity. If the inhibiting effect is so great that the protoplasmic machine cannot adjust itself to the new conditions, the higher its rate of activity, the sooner it is brought to a standstill. But if the inhibiting effect is slight, the higher the rate, the more rapidly and completely adjustment occurs, because adjustment depends, at least in large part, on the activity of the protoplasmic machine, that is, upon metabolism.

These relations between susceptibility and metabolic rate have been demonstrated in many different ways, and within certain

limits and with certain precautions can be used very widely as a means of comparing the general metabolic condition of different individuals, and of different regions of the body of a single individual. The method is so simple as to appear crude, but its delicacy and value have been shown very clearly. Practically it consists simply in finding the survival times of the different individuals or body regions to be compared in a concentration, determined by preliminary experiment, of the agents employed. I have found the cyanides particularly satisfactory for animals, because they are effective in very low concentrations and for various other reasons, but many other substances and conditions can be used in the same way.

In the two modifications of the method we have two ways of testing susceptibility and so of comparing general metabolic activity or fundamental features of it in different individuals and body regions. The first, in which susceptibility is directly determined by means of lethal concentrations, I have called the direct susceptibility method; the second, in which it is determined indirectly through the capacity for acclimation, I have called the indirect or acclimation method. The direct method is simpler and more satisfactory for most purposes, but can be controlled in many cases by the indirect.[3]

By means of these methods, checked and controlled by others, I have been able to demonstrate the existence of axial metabolic gradients as a characteristic feature of the animal organism, and various other lines of experiment indicate very clearly that the physiological axes are fundamentally metabolic gradients.

In my attempt to determine whether such axial gradients are present in plants the direct method was used, with the following procedure. The living plants, freshly collected, were first stained with the vital stain, neutral red, and then were placed in a solution of potassium cyanide in sea water. The neutral red was used as an indicator to make possible the determination of the time of death with some degree of exactness. In the plants thus stained and then killed in cyanide or various other agents of the proper

[3] These methods and some of their results have been considered in the following publications: CHILD, C. M., **4–10, 11** (particularly chapter iii), **12.**

concentration, the first indication of approaching death is an increase in the redness of the stain, indicating an increase in acidity in the cell. After this the red color rapidly disappears, often within a few seconds, or changes to yellow and then disappears. In the more transparent cells the disintegration and coagulation and disintegration of the protoplast, sometimes preceded by a rather sudden plasmolysis, can be observed directly. In these cases the protoplasm, which up to this time has appeared under low magnification to be uniformly stained, suddenly becomes turbid and contracts into a small irregular mass in the cell or a number of such masses scattered over the cell wall. These masses contain all the neutral red as well as the phycoerythrin in cases where it is present, and in consequence of the increased acidity and the aggregation of the protoplasm, these masses usually appear blackish or purplish by transmitted light. Beyond question the moment of this change is approximately the moment of death. The appearance of the cell is completely altered in many cases. Instead of being uniformly red, it now appears nearly transparent, except in cases where the cell wall is also colored, and contains one or more blackish masses or granules. Following these changes the color rapidly disappears from the blackish masses of coagulated protoplasm, leaving the whole cell almost transparent and without color except in the wall. These changes are most readily followed in the transparent hairs or hairlike branches which occur on many of the Rhodophyceae, where they can often be observed with great clearness. It seems probable that at least in some cases the neutral red is decomposed with loss of color in the course of the death changes, but in other cases it becomes yellow before disappearing because the alkali of the KCN solution penetrates as the protoplast dies. These various changes, the deepening red color of the stain, followed by its disappearance with change to yellow in some cases, the visible disintegration and coagulation of the protoplast, and finally in the red algae the loss of the natural color by the extraction of the phycoerythrin are very definite and striking, and afford a means of determining with a considerable degree of exactness the time of death of different cells of the plant and so their relative susceptibility.

After testing various concentrations of KCN, I found that although different species showed considerable differences in susceptibility, a concentration of $m/100$ served the purpose for the forms examined, the survival time in this concentration ranging from a few minutes to several hours.

Neutral red itself, particularly in high concentrations, is somewhat toxic to living cells, and in the course of my experiments I found that a strong solution of neutral red in sea water could be used in the same way as cyanide to determine differential susceptibility, the only difference observed being that death occurs much less rapidly in the neutral red alone than in cyanide.

The work was done at the Marine Biological Laboratory at Woods Hole during August and September 1915. From among the forms available at that time, species with definitely axiate, and in most cases with more or less highly branched thallus and with a more or less definite growing tip (at least during the earlier stages of growth), were selected, because it was desired first of all to determine whether characteristic differences in susceptibility were associated with the visible axes of stems and branches. Most of the forms examined were Rhodophyceae, and it might be supposed that the natural color of these forms would interfere with the use of neutral red as an indicator. As a matter of fact, however, the color of the protoplasm stained with neutral red is distinctly different from the natural color, and there was no serious difficulty in observing the change and disappearance of color in any case, and the protoplasmic changes afforded additional means of determining the time of death in many cases.

For the identification of a number of the species I am indebted to Mr. GUSTAVSEN of the M.B.L. Supply Department. Others were identified with the aid of FARLOW'S *Marine Algae of New England*, supplemented by RABENHORST'S *Die Meeresalgen*. Thus far the growing thalli or parts of them have been examined in 14 species.

The susceptibility gradients

Enteromorpha sp.—Many plants of this species were examined, ranging from stems and branches in very early stages of development to large old thalli which had taken on the "intestinalis"

characteristics. Young axes in good physiological condition always show a very definite susceptibility gradient from the apical end basally, that is, death with the disappearance of the neutral red begins at the tip of the stem or branch and proceeds basipetally with a high degree of regularity. The progress of the decoloration and death from cell to cell along the axis can be followed under the microscope. Occasionally a cell here and there or a small group of cells may die earlier or later than the other cells of their level, but in general the progress of death in the basal direction from the apical end is very regular in the younger axes.

In the large tubular axes, however, such a uniform death gradient does not appear. The first cells to die are scattered more or less over the whole length of the axis, or in many cases the death gradient is more or less distinctly acropetal in the more basal portions instead of basipetal as in the young axes.

These differences between the young and the large tubular axes are undoubtedly connected with the differences in the regions of growth and cell division in these different stages. In the newly formed developing axis where there is a more or less definite growing apical region, this is the region of greatest metabolic activity, and therefore a basipetal susceptibility gradient appears. Later, however, the activity of the apical region decreases and is apparently replaced by cell division and growth in the basal region or more or less along the whole axis. This change is associated perhaps with a greater or less degree of physiological isolation resulting from the decrease in activity of the apical region, which no longer dominates other parts to the same extent as earlier, and the earlier orderly behavior disappears. The original basipetal susceptibility gradient disappears, therefore, and is replaced by an acropetal gradient, at least in the basal region, or by a susceptibility mosaic. This method then makes possible an optical demonstration of the different localization of the highest metabolic activity at different stages. With a little care axes in all stages of this change can be found. In some the apical region is still active to some extent and a basipetal gradient extends for a short distance from it, while farther down the axis a susceptibility mosaic may appear, or the basal region may show a high susceptibility.

When the plant is killed by a high concentration of neutral red alone, the same axial differences in susceptibility appear as in death from KCN, although of course death begins later and progresses much less rapidly. The simple experiment of gradually killing the plants by overcrowding in standing water was also performed, and the changes in susceptibility and the progress of death were followed. After two days under these conditions, staining with neutral red showed that longer or shorter portions of the apical regions of the small short branches were dead and would no longer take the stain, while other parts still stained as living cells. In the large tubular thalli practically all cells were still alive at this time. After 5 days in standing water most of the short young branches were wholly dead, but in some a short basal region was still alive. The large thalli at this time showed a mosaic or patches of dead cells, often more marked in the basal region. These crude experiments are sufficient to show that differences in the susceptibility of different regions of the plant to overcrowding in standing water are essentially the same as to KCN. Death progresses in the same way in both cases.

One other point of interest in relation to the physiological age of parts may be mentioned. I have found it possible to use the susceptibility method very widely among animals to distinguish differences in physiological age, the young animals being more susceptible than the old because of their higher metabolic rate (11). In *Enteromorpha* the short branches, evidently in early stages of development, are more susceptible than the larger older branches. Where such short branches arise laterally on a larger stem, death proceeds basipetally in the short branch to the point where it joins the stem, but here it stops for the time being and the adjoining cells of the stem may remain alive for several hours after the branch is dead. The branch is evidently much younger than the stem at its level, and consists dynamically of a metabolic gradient of much higher rate than that of the stem, and this gradient ends rather sharply at its base. The gradient in the branch itself is also in a sense an age gradient, the cells of the apical region being youngest physiologically because of their continued reproduction, while basipetally the physiological age of the cells increases. In the large

thalli where growth is no longer apical but more or less generally distributed, cells here and there have undergone more or less dedifferentiation, and so have become younger and resumed reproduction.

Where a thallus has been broken or injured, an area of high susceptibility extends for a greater or less distance, often 0.5 mm. or more from the region of injury. In the younger portions of the thallus where the basipetal gradient is still present, this area of high susceptibility arising from an injury extends farther in the basal than in the apical direction. Evidently this area represents the extent of the stimulation resulting from the injury, or at least the more persistent component of it.

The visible changes in the single cells as death approaches are essentially those described in the preceding section. First the color of the stain deepens, beginning in the young branches at the apical end and proceeding basipetally. Then as the protoplast undergoes disintegration and coagulation at death, the cell contents appear as an irregular blackish mass, but from this the color soon disappears and the dead decolorized cell is yellowish green instead of green under low powers, while under high powers the coagulated masses of protoplasm are visible.

The susceptibility method can undoubtedly be used for analyzing the metabolic conditions in *Enteromorpha* and related forms to a much greater extent than the few experiments described here indicate. As regards the question of metabolic gradients, however, these experiments give a definite answer. They show that the vegetative individual is dynamically in its earlier stages such a gradient, that each new branch is a new gradient and so a new individual, and that with advancing age and under certain environmental conditions the gradient may disappear more or less completely and give place to a mosaic of more active regions scattered over the thallus or more distinct basally.

Ectocarpus confervoides.—In this form the branches which are younger as regards development and the more apical regions of most others show a distinct basipetal gradient, while in the more basal regions of the more advanced parts of the thallus considerable irregularity appears, some cells dying earlier or later than

in a regular basipetal gradient. These irregularities undoubtedly indicate the disappearance of the regular gradient in the later vegetative stages, with intercalary growth and cell division in the more basal regions. Here, as in *Enteromorpha*, elongation of the axis beyond a certain length, or decreasing activity of the apical region in consequence of advancing physiological age or for other reasons, may lead to a greater or less degree of physiological isolation of the more basal cells, which then again become active and therefore show a higher susceptibility.

Castagnea tuberculosa.—The complex structure and opacity of the thallus of this form interfered with the use of the susceptibility method, but it was found that the apical regions were most susceptible, and here in many cases the cells actually disintegrated in KCN as they do soon after death in many of the lower animals. Over most of the length of the thallus, however, no definite and constant gradient was observed.

The delicate transparent hairs which arise on the surface of the thallus afford interesting objects for susceptibility experiments. They consist of a single series of elongated cells and are unbranched. These hairs are very highly susceptible to KCN, and in $m/100$ they begin to die almost at once. Most hairs show in general a basipetal susceptibility gradient, but there are frequent irregularities, one or a few cells dying out of the order proper to such a gradient. Many if not all of these irregularities are undoubtedly due to injuries, for the hairs are so delicate that even the most careful handling of the plant is likely to break or bend them, but it may be that other factors are also concerned. The usual susceptibility gradient in these hairs indicates that their growth is primarily apical like that of most plant axes, but it is not improbable that in later stages secondary growth and division may occur in other cells as the activity of the apical region decreases.

Callithamnion (roseum?).—This monosiphonous form is very favorable for demonstration of axial differences in susceptibility. Both young plants consisting of a single stem with bipinnately arranged branches and more advanced stages in which branching had proceeded much farther were examined with similar results in all cases. In each branch death begins at the apex and proceeds

basipetally from cell to cell. In each bipinnate system of stem and branches death begins at the apex of the stem and the most apical branches, and proceeds basipetally in the whole system, that is, the branches nearest the apex of the stem are most susceptible, those lower down are less susceptible, and so on to the base of the bipinnate system. The apex of the main stem of such a bipinnate system is highly susceptible like the apical branches, but the susceptibility decreases rapidly down the stem, so that at any level the stem is less susceptible than even the basal regions of branches at that level. These susceptibility gradients are remarkably regular and uniform with one characteristic exception. In the older more basal branches and in the stem of each bipinnate system of the thallus it was observed that the basal cell or the two most nearly basal cells were usually somewhat more susceptible and died earlier than the next two or three cells apical to them. In other words, the gradient in such branches is basipetal except for one or two cells at the base. The greater susceptibility of these basal cells suggests the possibility that they are the seat of secondary growth activity in consequence of physiological isolation, as in *Ectocarpus*, but whether this is actually the case or not I do not know. It may be merely that these cells are subjected to greater mechanical stimulation than more apical cells as the branches bend with water movements.

The greater susceptibility of more apical as compared with more basal branches in the same bipinnate system is undoubtedly due to the fact that the more basal branches are physiologically older and their rate of metabolism is lower than that of the more apical branches.

Pleonosporium Borreri.—Only very young plants of this species, consisting of a single unbranched axis of a stem with a few lateral branches, were examined. In every case a distinct basipetal susceptibility gradient was found, both in the main axis and in the lateral branches when they were present.

Ceramium rubrum and *C. tenuissimum.*—The susceptibility gradients in these two species are distinctly basipetal. The small cells of the extreme apical region are distinctly more susceptible than the larger differentiated cells below, but in the differentiated region the gradient is very regular for a distance of several milli-

meters from the apical ends when the plants are in good condition. In the more basal regions of the older, highly branched thalli, however, more or less irregularity usually appears, death occurring at the same time over lengths of 2 or 3 mm., or certain levels of the stem showing a higher or lower susceptibility than adjoining regions. Many very young unbranched individuals of *C. rubrum*, ranging from only 6–8 to 30–40 cells in length, which were found growing on other algae, were examined *in situ* and therefore in wholly intact condition. In these the basipetal susceptibility gradient was found to be very regular, and in the shorter individuals it extended to the base of the plant, while in some of the longer, some slight irregularity appeared in the basal region. As might be expected from the dichotomous branching in *Ceramium*, the susceptibility of all apical regions from the same general portion of a highly branched thallus was found to be about the same, except that in various cases where one member of a pair of young branches had been retarded in its development, the susceptibility of the retarded member was slightly less than that of the other. Different regions of the thallus, however, may show somewhat different susceptibilities even in the apical regions. For example, the lower peripheral portions of a large, highly branched thallus are often less susceptible than the upper parts, probably in consequence of different environmental conditions. *C. rubrum* is rather resistant to laboratory conditions as compared with other forms; the apical regions retain their susceptibility and the gradients persist with little or no change, even after a day or two in standing water.

The differences in susceptibility along the axis in *C. rubrum* are such that it requires several hours in KCN *m*/100 for death to progress from the growing tip to a level 3–4 mm. below it. In young unbranched plants about 20 cells in length, the progress of death over the whole length of the plant required about an hour in cases observed. In a few cases the progress of death from cell to cell was followed and timed for some distance. In the younger plants and the more apical regions of older axes the length of time between the death of one large cell of the axis and the next basal to it is only 2–3 minutes, while in more basal regions, where the metabolic rate is lower, it may be 15–20 minutes. The collapse and

disintegration of the protoplast and the disappearance of color take place in a few seconds. In neutral red alone the axial differences in susceptibility are similar to those in KCN, but death begins much later and proceeds more slowly.

A few observations were made on the transparent hairs which arise from the cortical cells. These hairs contain no transverse cell walls, being merely cell outgrowths. In the long fullgrown hairs the susceptibility gradient is distinctly acropetal, while in those which are apparently still growing, it is basipetal. These differences suggest that while the hair is growing its apical region possesses the highest metabolic rate and the axial gradient is basipetal, but that after growth is completed and the apical activity decreases, the gradient becomes acropetal, that is, from the cell with which the hair is connected. The possible significance of this change will be considered later.

Spyridia filamentosa.—Observations on this form are fragmentary, since only a single thallus, detached and apparently not in perfect condition, was available for examination. Each main branch of the thallus, as well as each of the simple lateral branches which arise from it, shows in general a basipetal gradient; and each such system as a whole shows more or less clearly a basipetal gradient from branch to branch, the most apical branches being most susceptible, the next lower in general less so, and so on.

In the plant examined, however, irregularities in these gradients were frequent, both in single branches and in the whole system. Here and there cells were already dead, while others were more or less susceptible than their neighbors, and the same differences appeared between different branches in some cases. These irregularities probably indicate that the plant was not in good physiological condition; as previously noted, it was detached when collected and had been washed about by the waves, so that some of the cells had undoubtedly been injured or killed. The susceptibility of this species to KCN and to neutral red is in general very high, death beginning almost at once in KCN $m/100$, and within half an hour to an hour in neutral red alone. Since I have found that high susceptibility to the cyanides in animals indicates in general high susceptibility to at least many other depressing

conditions, I am inclined to regard this species as rather sensitive and readily injured physiologically, and such a high susceptibility would readily account for the irregularities observed in the death gradient.

Champia (*Chylocladia*) *parvula*.—Various stages of development, ranging from unbranched to large much branched thalli, were examined. In general, death begins at the apical end of each axis. A short terminal portion, evidently representing a growing tip, dies first, and then, after a more or less distinct interval, death proceeds slowly basipetally. In the younger, shorter axes the gradient is usually very regular over most of the length, and in the older axes over the apical 2–3 mm. Farther basally, however, irregularities appear in cells or cell groups. Whether these irregularities indicate physiological isolation and secondary growth in these basal regions, or whether they are the result of injuries or other external factors, I do not know. They are certainly more frequent in the longer, older axes than in the shorter, younger ones. In general also the younger axes, or at least their more basal regions, show a higher susceptibility than the older axes, so that while the death of the growing tip may occur at about the same time in both, the basal region of the younger branch may die considerably earlier than that of the older branch.

The transparent, unicellular hairs which develop on the thallus usually show an acropetal susceptibility gradient in the cases examined, like the hairs of *Ceramium rubrum*, although in some hairs the gradient is basipetal and in some death begins at both ends and proceeds toward the middle. Further observations are necessary to determine with certainty the meaning of these differences, but it seems probable that, as in *Ceramium*, the growing hair may have a basipetal gradient, the full grown hair an acropetal gradient, and that those in which death begins at both ends are stages in the change from one condition to the other. It may be, however, that stimulation or injury is responsible for these differences in some cases at least.

Chondriopsis (*Chondria*) *dasyphylla* var. *sedifolia*.—In young unbranched or slightly branched plants in good condition and usually in the more apical regions of the branches in older much

branched thalli, the susceptibility gradient is basipetal. Irregularities in the course of death and acropetal gradients observed in some cases probably result from injury or bad environmental conditions which affect the more active regions to a greater extent than the less active regions, or they may indicate perhaps the completion of apical growth in an axis. In general the physiological ages of different branches on a single axis are indicated by their susceptibility, the smaller less advanced branches being the more susceptible.

In some of the plants examined cystocarps were present. In the sterile wall of the cystocarp the gradient is basipetal, as in the vegetative portions of the plant. Differences in susceptibility in the cystocarp contents, indicating differences in physiological age, were also observed. No attempt was made to distinguish the various stages in the development of the carpogonium and carpospores, but it was merely noted that the susceptibility of the fully developed carpospores was much less than that of the cystocarp contents in the earlier stages. This difference indicates that the carpospore has the low metabolic rate characteristic of physiologically old cells.

The transparent hairs which arise in tufts at the apical ends of the thallus branches are beautiful objects for the observation of the susceptibility gradient. Each hair is monosiphonous and dichotomously branched, and the susceptibility gradient in each hair as a whole is very distinctly and uniformly basipetal, the apical cell of each branch dying first and death progressing basipetally from cell to cell in regular order.

In each single cell of the hair, however, the susceptibility gradient is almost invariably acropetal. The disintegration of the protoplast and the appearance of the dark masses resulting from coagulation begin at the basal end and proceed very uniformly to the apical end of the cell, the progress of death over the whole length of the cell often requiring 2–3 minutes. With rare exceptions the death of each cell is completed before that of the next cell basal to it begins.

My observations were limited to hairs which were apparently full grown or nearly so, and only further work can determine

whether young actively growing hairs will show the two opposed gradients or not. Discussion of the facts is postponed to the general section of the paper.

Polysiphonia variegata and *P. fibrillosa*.—In *P. variegata* the general axial gradient is clearly basipetal in each axis, with a few irregularities in freshly collected plants. The transparent, dichotomously branching hairs also show a basipetal gradient, both in the hair as a whole and in the single cells, so far as observed. After a day or two in the laboratory irregularities in the susceptibility are much more frequent.

Cystocarps in various stages of development were present on some of the plants examined, as in *Chondriopsis*. The cystocarp wall shows a basipetal gradient. In general the susceptibility of the cystocarp, except in the earliest stages of its development, is lower than that of the cells of the vegetative axis from which it arises, and it was further noted that the region of the branch to which the cystocarp is attached also shows a lower susceptibility than adjoining regions of the axis. This low susceptibility may extend basipetally over 4 or 5 segments of the thallus, and acropetally over 2 or 3, and is more marked in connection with more advanced than with earlier cystocarps. Apparently the cystocarp in its later stages, together with a portion of the vegetative thallus in the region of its attachment, represents a region of lower metabolic activity than the adjoining vegetative regions.

As in *Chondriopsis*, the cystocarp contents in the earlier stages are much more susceptible than the fully developed carpospores which are the least susceptible portions of the whole plant on which they occur. Apparently metabolic activity in the carpospores is relatively slight.

P. fibrillosa is in general much more susceptible then *P. variegata*, and after a few hours in the laboratory the course of death along the axes is very irregular. In freshly collected plants, however, a basipetal gradient usually appears clearly in the more apical regions, but even here the irregularities are very frequent a few millimeters from the tips, and sometimes death occurs first at some level below the tip. I think it probable that these irregularities result from stimulation or injury of the apparently very sensitive

cells in collecting and handling. The great difference in susceptibility between the two species is evident from the fact that in *P. fibrillosa* death begins almost at once and is usually completed within a half hour or less in KCN *m*/100, while in *P. variegata* even the more apical regions live in the same concentration from half an hour to an hour, and the less susceptible parts die only after several hours.

Dasya elegans.—In both the polysiphonous axes of the thallus and the very numerous monosiphonous, dichotomously branched secondary branches, the susceptibility gradient is in general distinctly basipetal. In the secondary branches, however, irregularities appear, chiefly near the base. As in *Callithamnion*, the basal cell or the two most basal cells of the older branches very often die before those above them. The suggestion made in the case of *Callithamnion* may apply here also, namely, that these cells are more stimulated mechanically than those above them by the movements of the branch with the water currents. It may be, however, that some degree of physiological isolation of the basal region has occurred in the older branches.

A basipetal gradient also appears in the system of secondary branches on an axis as a whole, the most apical branches being most susceptible, those lower down less so, and so on. This is true even for the apical regions of the secondary branches, and indicates their differences in physiological age, corresponding in general to their level on the axis, the most apical being the youngest, the most basal being the oldest.

The elongated stichidia present on some of the plants examined also show a basipetal susceptibility gradient, and the gradient in development of the tetrasporangia in the stichidia is paralleled by a susceptibility gradient, the most basal and so most advanced tetraspores being the least susceptible parts of the plant on which they occur.

Discussion

The observations on these 13 species indicate, so far as they go, that in each definite vegetative axis of these forms, at least in plants that are in good condition and not too old, a more or less definite

susceptibility gradient exists. To these may be appended some fragmentary observations on the blue-green alga *Calothrix*, which indicate that even in this simple form a basipetal susceptibility gradient exists. Although the observations are incomplete at many points and further work on other stages and species is necessary, the uniformity of results is striking and cannot but suggest that the order observable along these axes and the susceptibility gradients are in some way associated. If the susceptibility method is of any value as an indicator of general metabolic or oxidative activity, the susceptibility gradient represents a gradient in metabolic or oxidative activity, the most susceptible regions being the most active. If this be true, the axes of these simple plants possess primarily the same metabolic characteristics as the axes of animals in this respect. Such a fundamental resemblance or rather identity as this must possess some fundamental significance, and in the introductory section of this paper my views concerning this significance are briefly stated. Many lines of evidence have forced me to the conclusion that this axial metabolic gradient is the basis, the starting point of the order in space and time which is characteristic of the axes of organisms. In short, according to this point of view, the axis, whatever else it may become during development, is fundamentally a metabolic gradient. The order along the axis is primarily an expression of this gradient. The organic or physiological individual, as distinguished from other kinds of individuality which may exist in the organism and in the inorganic world, consists fundamentally of one or more metabolic gradients. The various aspects of this conception of the organic individual and their bearing on biological problems have been considered elsewhere (**12**), and it is impossible here to do more than note the complete agreement with the general conception of these observations on plants.

From this point of view there is a fundamental identity in the apical regions of plant and animal organisms and in their relations to other parts. I have suggested elsewhere (**12**, pp. 189–192) that the fact that the apical region of the animal gives rise to the highly specialized and physiologically stable cephalic nervous system or brain, while that of the plant remains indefinitely or for a long time

more or less completely embryonic, must be connected with certain differences in the metabolic processes in the two groups. Morphological structure in the animal is to a large extent primarily colloid and protoplasmic, while in the plant the structural substances are mainly carbohydrates, and the protoplasm itself shows little permanent or persistent structure. Apparently in plant metabolism the proteids and other protoplasmic substances produced are less stable under physiological conditions than in the animal, and so do not persist as structure but are continually undergoing change and reconstitution, particularly in regions of high metabolic activity. In the animal, on the other hand, some relatively stable molecules arise even in regions of the highest activity; consequently morphological structure appears, even in these regions, and such structure is more stable than structure developed in regions of lower metabolic rate. Because of these differences the apical region of the animal undergoes differentiation, and its relations to other parts determine that this differentiation shall take the form of a transmitting system, the nervous system, which brings about a high degree of physiological integration, while in the plant the apical region usually remains embryonic or differentiates very slowly. Transmission exists only in relatively primitive form and the degree of physiological individuation in the plant remains low.

In the unicellular hairs of *Ceramium* and *Champia* the susceptibility gradient is usually acropetal in the full grown hairs, but apparently basipetal in the growing hairs and in the multicellular branching hairs of *Chondriopsis* the gradient of the hair as a whole is basipetal while that of single cells is acropetal in the full-grown hairs. In the multicellular hairs of *Castagnea* the gradient is usually basipetal, but a distinct intracellular gradient could not be distinguished. Further work is necessary for positive conclusions, but a suggestion is perhaps permissible. These hairs of course are incapable of photosynthesis and are dependent, therefore, on other parts of the plant for nutrition. The course of nutritive substances must therefore be acropetal in direction in them. In view of the facts available, it seems probable that during the growth of the hair the apical region has the highest metabolic

rate and the gradient is basipetal. Under these conditions each level lives, so to speak, at the expense of the level or levels basal to it. At this stage the gradient is probably basipetal throughout, at least in some cases; but as senescence progresses and the activity of the apical region decreases, the nutritive factor may become more important in determining the metabolic rate at different levels. Since the direction of movement of nutritive substance must be acropetal in each cell, the basal portions of the cell are most favorably situated and perhaps therefore show a higher metabolic activity with an acropetal gradient, provided relations to more apical cells do not obliterate or reverse it. In this way a gradient in the cell opposite in direction to the gradient in the hair as a whole may arise, at least in the later stages of development. It may be that in some of the multicellular hairs this condition is present from the early stages of development, but the fact that in the unicellular hairs of *Ceramium* and *Champia* the gradient is basipetal in what appear to be the earlier stages of development, and acropetal in the fully developed hairs, indicates that such change may occur. It remains, however, for future investigation to determine whether these suggestions are correct.

Attention has been called incidentally to the differences in susceptibility which apparently indicate differences in physiological age, such, for example, as the lower susceptibility of fully developed as compared with small developing axes, and the low susceptibility of the carpospores. The basipetal axial gradient itself is in a sense an age gradient, for the physiological age of the cells increases from apex to base, the apical cell or cells remaining physiologically young because of continued division and cell reproduction, and the other cells differentiating and growing old more or less rapidly according as they divide less or more frequently. We may say in fact that the axial gradient is a more or less definite gradient in cell behavior, and it is this which must be accounted for. It is here, as I believe, that the physiological dominance of the apical region plays a rôle. This region is the first part of the axis to appear, and it originates as a region of high metabolic activity, either in consequence of physiological isolation from other apical regions or by the local

action of external factors. After it has once arisen it becomes, as I have endeavored to show, the chief factor in determining the metabolic rate in the other regions of the axis to which it gives rise, so far as they are within the range of its influence. Since the changes transmitted from it to other regions undergo a decrement in energy or effectiveness in the course of transmission, a more or less definite gradient in metabolic activity and therefore in behavior of the cells results. The more active cells divide more frequently and differentiate and grow old less rapidly than the less active cells. The apical region itself, as the most active region of all, may remain embryonic and physiologically young indefinitely if the processes of senescence and rejuvenescence balance each other in it; but if this is not the case it may gradually grow old, though senescence is less rapid in it than in other parts because of the higher metabolic rate. According to this conception, therefore, an apical region arises wherever the metabolic activity of a cell or a cell group, or in unicellular forms of a part of the cell protoplasm, becomes high enough to enable it to dominate or control to some degree the metabolic activity of other cells within a certain range. When the apical region has arisen, the development of the plant or animal individual proceeds as the specific constitution of the protoplasm and the conditions determine.

As soon as differences between different parts along the gradient arise, chemical correlation, that is, the influence of substances produced in one part upon another, must begin to play a part, and this is unquestionably a factor of great importance in determining the further course of events along the axis. It is evident, however, that chemical correlation cannot occur in an orderly way unless orderly differences already exist at different points or levels, and I have endeavored to show how these differences may find their origin in the axial metabolic or irritability gradient (12). If my conclusions are correct, the physiological axes in both animals and plants consist in their simplest form of such a gradient, and it is the interrelation or correlation in this gradient which determines the orderly behavior in relation to this axis.

Summary

1. In 14 species of marine algae, including 10 species of Rhodophyceae, 2 of Phaeophyceae, 1 of Chlorophyceae, and 1 of Cyanophyceae, a more or less definite gradient in susceptibility to KCN exists in the vegetative axes, and in several species in other parts also; the susceptibility being greatest, at least during growth and development, in the apical region and decreasing basipetally.

2. Since extended experiment with the lower animals indicates that the degree of susceptibility to cyanides and to many other agents and conditions is in a general way, and within certain limits, a rough measure of metabolic activity or of certain fundamental metabolic processes, probably primarily the oxidations, these axial differences in susceptibility in the algae are regarded as indicating the existence of axial metabolic gradients. If this conclusion be correct, the axis in these simple plants is identical with the axis of the animal organism in this respect.

3. The relations of physiological dominance and subordination, of physiological isolation and of differentiation to metabolic gradients, are briefly considered.

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THE VASCULAR ANATOMY OF PIPER METHYSTICUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 218

RACHEL E. HOFFSTADT

(WITH TWENTY-THREE FIGURES)

Historical

LINNAEUS placed the Piperaceae in the monocotyledons among the Aroidaceae; JUSSIEU held that they were near the Urticaceae; KUNTH (8) and BLUME ranked them with the monocotyledons. DE CANDOLLE (4), however, following JUSSIEU, stated that the embryo characters indicated their dicotyledonous character. ENGLER and PRANTL (5) put the tribe Piperales among the lower Archichlamydeae. Included in it are 4 families: Saururaceae, Piperaceae, Chloranthaceae, and Lacistemaceae. The genus *Piper* contains over 1,000 species. MIQUEL (10) separates 7 species from the original classification on the basis of the presence or absence of his so-called "stipula oppositifolia" and persistence of the petiole. Among these is *Piper methysticum* Forst., which he calls *Macropiper methysticum*. ENGLER and PRANTL (5), using as a basis of their classification of these two genera the method of branching in the floral regions, retain the name of FORSTER.

Piperaceae have attracted much attention because of their anomalies, both in anatomical and reproductive features. The former have been described in many species. MIQUEL (10) asserted that the internode of the stem ends blindly in the petiole, and the next internode develops from a bud between the petiole and the end of the foregoing node. He stated also that there are alternate, opposite, and whorled leaves on the same branch. The latter he concluded were atrophies, and the number of internodes which would have been produced would have been the same number as the whorls of leaves. SANIO (11) described in detail the structure and the course of the bundles in the stem of *Peperomia blanda*. SCHMITZ (12) verified the work of SANIO in *Peperomia*. He concluded that the peripheral bundles in *Piper* were joined at

their base with the inner bundles of the stem. The small bundles of the leaf trace come from branches of the peripheral bundles. They, as well as the central bundles, go with or without branching into the petiole, which is merely a continuation of the stem.

In an elaborate discussion of the vascular anatomy of the Piperaceae, WEISS (**19**) deals with 11 species of *Peperomia* and 8 of *Piper*, and draws the conclusion that in the Piperaceae there is a transition from the monocotyledonous to the dicotyledonous type of bundle.

By far the most detailed account is that of DE BRAY (**3**). He used 4 species of Saururaceae, 16 species of *Piper*, 3 species of *Artanthe*, and 11 species of *Peperomia*. In *Piper* he found 2–4 rings of bundles arranged in two systems, the peripheral and the pith systems. The peripheral bundles are of two sizes; the outer ring is completed by an interfascicular cambium; the leaf trace comes from a peripheral ring, which in the node below is a branch of the central bundles; the vascular supply of the axillary buds is from both peripheral and central bundles. He compares the families of the group, but shows no relationships.

In VAN TIEGHEM'S (**17**) work on the mucilage canals of *Piper* he describes in detail the stem of *Piper nigrum*. He found that there are two circles of bundles; that the pericycle becomes lignified late in the growth of the stem; that the cambium for a long time cuts off segments only on the side toward the pith, and may cut off very late a few segments on the other side; that the mucilage canals vary in location with different forms and are not continuous through the nodes; and that the canal of the petiole is not continuous with that of the branch.

The present study of *Piper methysticum* was taken up with the idea of giving a modern interpretation to the vascular structure, and to ascertain whether the stem keeps pace with the gametophyte of the group.

Material

I am indebted to Dr. W. J. G. LAND for the material for this study. It was collected on the Island of Tutuila, Samoa (fig. 1). The plant is a native of the South Sea Islands, and is commonly

called *Ava* or *Kava*, the natives extracting from its roots the national beverage bearing that name.

It becomes a shrub 1–1.5 m. in height and is propagated mostly by cuttings. No seedlings were obtainable. The leaves are ovate, 18–25 cm. in diameter, with a deep cordate base and a short accuminate apex. The blade is bright green, smooth above, and bears fine multicellular hairs on the veins beneath. It is distinctly petioled, the petiole having a sheathing base and

FIG. 1.—*Piper methysticum* growing in Samoa

a deciduous stipule. The leaves are alternate and the dense flower clusters are borne opposite them. The internodes are 7–10 cm. long, the nodes being swollen, smooth, and in the older ones irregularly spotted. Both old and young stems have an herbaceous appearance. The largest nodes examined were 2.75 cm. in diameter, and the smallest were 2 mm.

For the sake of comparison *Piper umbellatum* (*Heckeria umbellata* Kunth) was used, the material being obtained from plants brought from Mexico. In shape and size the leaves resemble those of *Piper methysticum*. The petiole has a sheathing base;

the nodes are swollen and marked with several distinct rows of spots; the internodes are 5–9 cm. long and when young are covered with dense rows of hairs, giving a ridged appearance; the older internodes are smooth but spotted.

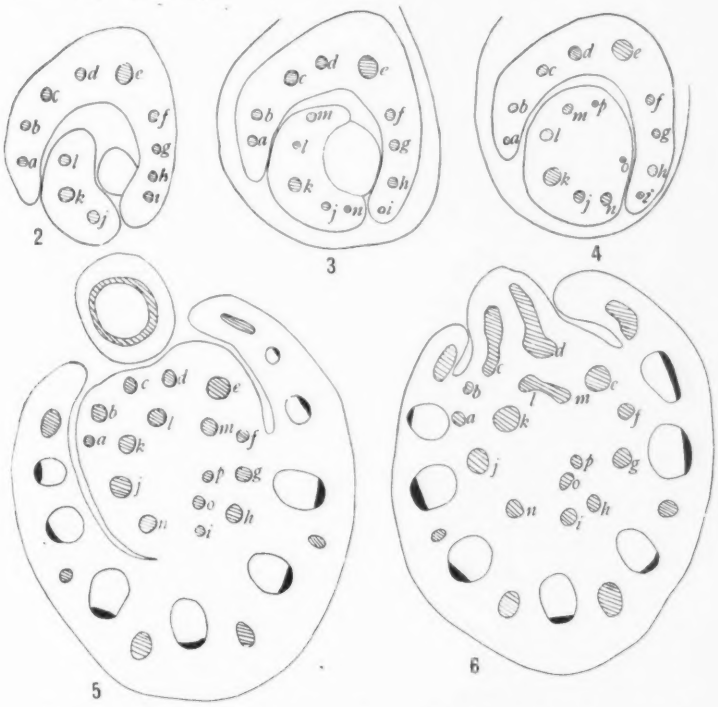
The younger stems and nodes were cut in paraffin at 25–30 μ and complete series obtained. The largest stems and nodes were treated with hydrofluoric acid for one week and then sectioned at 30–50 μ with a sliding microtome, in this case also the series being complete. The safranin Lichtgrün stain was used.

Origin and course of stem bundles

The stem of *Piper methysticum* contains at maturity three rings of bundles, one peripheral and two within the pith, the bundles being foliar. The terminal bud is enveloped in the sheathing base of the youngest leaf. In some cases a bud was found within the sheath of a single leaf with as many as 3 leaves, each of which was inclosed in the base of the petiole just beneath it.

The leaf primordium appears on the stem tip early and forms about it a semicircle, and 5–7 procambial strands are soon differentiated. These connect with the first strands of the stem (figs. 2–4, *j–p*). Strands *j–p* are the strands of the youngest leaf (node 1); *k* is the first to be differentiated; *j* and *l* follow quickly; *o* and *p* come last. The bundles of the second leaf (node 2) are represented by the series *a–i*. At node 1 the stem contains a single row of scattered bundles. These bundles (*j–p*) become the inner bundles of the stem at node 2, and *a–i* of leaf 2 become the peripheral bundles (fig. 5). Through the following internode these two sets of bundles run approximately parallel and become the inner rings of the next node (node 3, fig. 6). The union of the two inner rings takes place here. Five methods of joining were observed in the case of the undifferentiated strand: (1) two strands from the same ring may join (fig. 8, *lm*); (2) two strands from different rings (fig. 7, *ak*); (3) one strand may divide and join a strand of a different ring (fig. 7, g^1p); (4) two strands from the same or different rings may unite and then join a branch of a strand from either ring (fig. 9, *efg*, *ino*); (5) three strands may join, the result of this, for a short time, being a single inner ring (figs. 9, 10, *dlm*).

The peripheral bundles at any node may branch. In older nodes this branching may occur just before the peripheral bundles become pith bundles, and part remain in the peripheral ring; the latter will then connect with the bundles of the leaf at the node below (fig. 19).



FIGS. 2–6.—Transverse section through a terminal bud of *P. methysticum*, showing the course of the bundles; ×168.

The coalescence of the branches of these bundles does not always occur at the node, but may occur above or below it, as follows: (1) branches of the same bundles may join before passing through a node; (2) branches from different bundles may unite; (3) branches of a peripheral bundle of the internode above may join a peripheral bundle of the internode below. Not infrequently strands isolated in the anastomosing of the pith bundles at any

node may join the peripheral bundles at that node. The peripheral bundles of any internode, therefore, when young will consist of one set of foliar bundles only; and when older may contain portions of the foliar bundles of the leaves of 3 nodes.

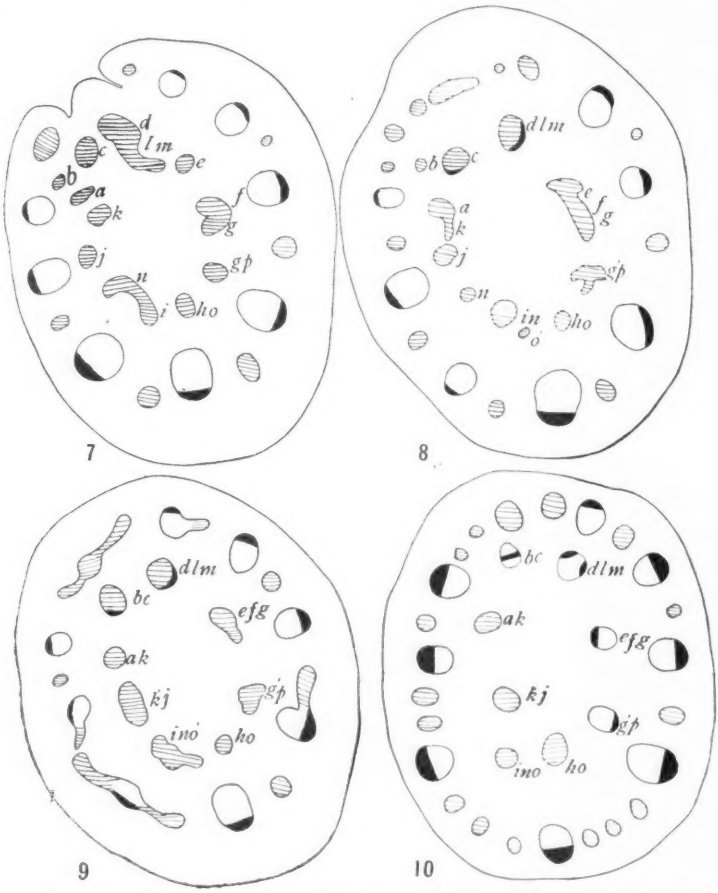


FIG. 7–10.—Transverse sections through a terminal bud of *P. methysticum* showing course of bundles; sections follow those of figs. 2–6; ×168.

The node in which the strands have become differentiated presents a most complicated appearance. One often finds for

a short time xylem entirely surrounding phloem, and vice versa. Bundles may join with either the phloem or xylem together. They may lie side by side and union may occur either in the xylem or in the phloem. Not infrequently the xylem of two bundles may unite, and the phloem of a third join the phloem of either of the others. Strands become separated from bundles and several of these may coalesce to make a bundle, or they may join with other bundles. One often gets cross-sections and longitudinal sections of the same bundle in the same section.

The bundles in one internode are in the periphery, and through the following two internodes are pith bundles. The position in the pith often gives the appearance of two complete rings and one-half of a third ring, when the number of bundles is large; but careful study shows that there are really only two rings. The number of bundles reaches 45–50 in the pith.

Description of stem in detail

As previously stated, the stem of *Piper methysticum* has two sets of bundles which may be designated as the peripheral ring and pith or medullary rings, two in number, and an irregular half-ring which gives the appearance of a third ring at times. The bundle type is open collateral endarch, oriented for the most part in the usual manner. Sometimes, however, one finds the protoxylem points appearing in reverse orientation (fig. 10, *e–g*). Union is often incomplete and one finds double bundles persisting in the internode, and these may be of two types. The xylem points or the phloem points may be together (figs. 11, 12).

The peripheral ring of bundles is formed of two sizes: the primary, those differentiated first; and the secondary, termed supplementary by De Bray (**3**) (fig. 13). The secondary bundles are branches of the primary bundles and lie between them. More than one primary bundle may contribute to a secondary one (fig. 9); that is, two bundles may branch and the branches join. The number of secondary bundles varies from none to 3, according to the age and size of the stem. Near the tip there are none (fig. 4), as observed by Schmitz (**12**).

The inner rings of bundles are approximately the same size. This does not differ from the majority of the species of *Piper*.

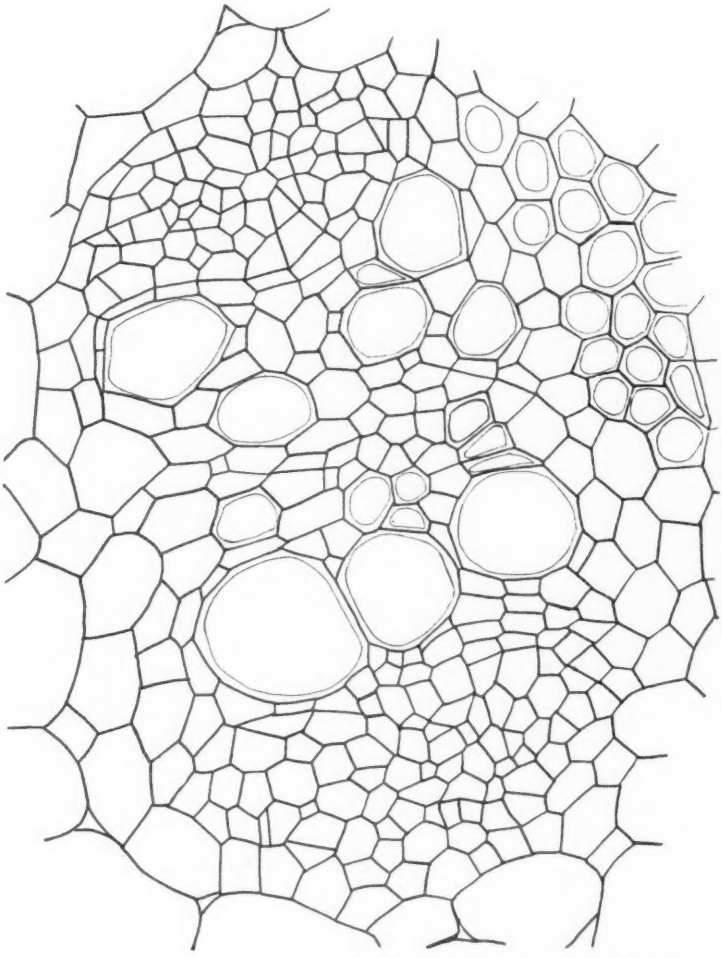


FIG. 11.—Detail of a double bundle with phloem on the outside and lignified tissue at the side; ×820.

Between the pith and the peripheral ring of bundles in the young stem is a continuous band of parenchyma, 4–6 rows thick, which

early becomes lignified (figs. 13, 14). Later, owing to growth of the bundles, this band is broken and patches appear only at the inner portions of the bundles (fig. 18).

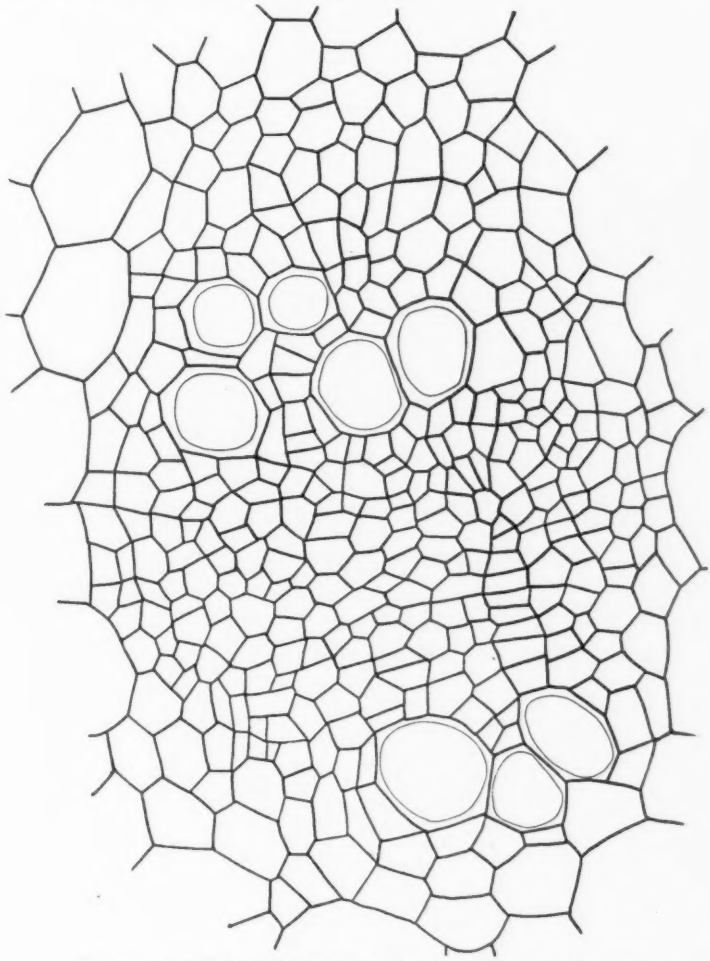
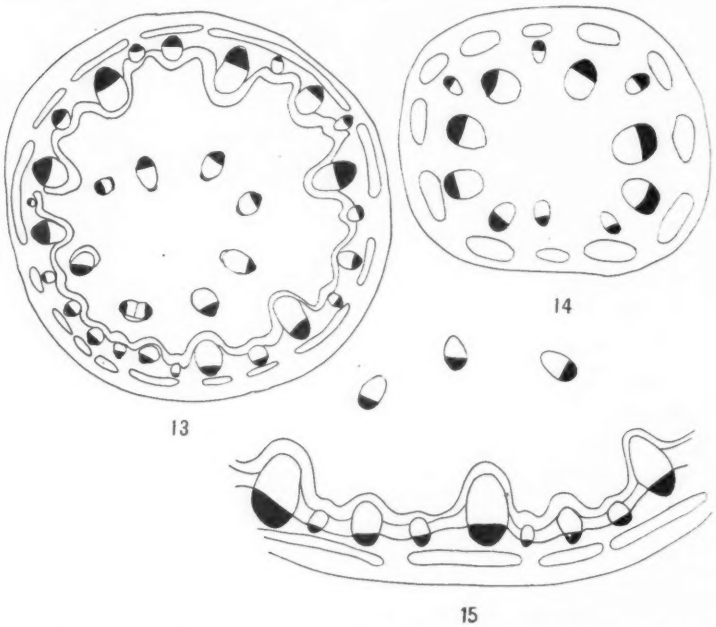


FIG. 12.—Detail of double bundle with xylem points outside; ×820

The pericycle consists of only a few cells (fig. 16) just outside the bundles in both the peripheral and pith systems, and nowhere else. It can be distinguished easily in the young stems by the

dense cell contents. Late in the history of the plant the pericycle becomes lignified. There is no differentiated endodermis in either old or young stems.

In the cortex of the young stem is a continuous band of tissue 7–8 cells wide, which responds to the test for suberin (TUNMANN **16**). This is in patches in the older stems. The intercellular spaces of the pith are very large.



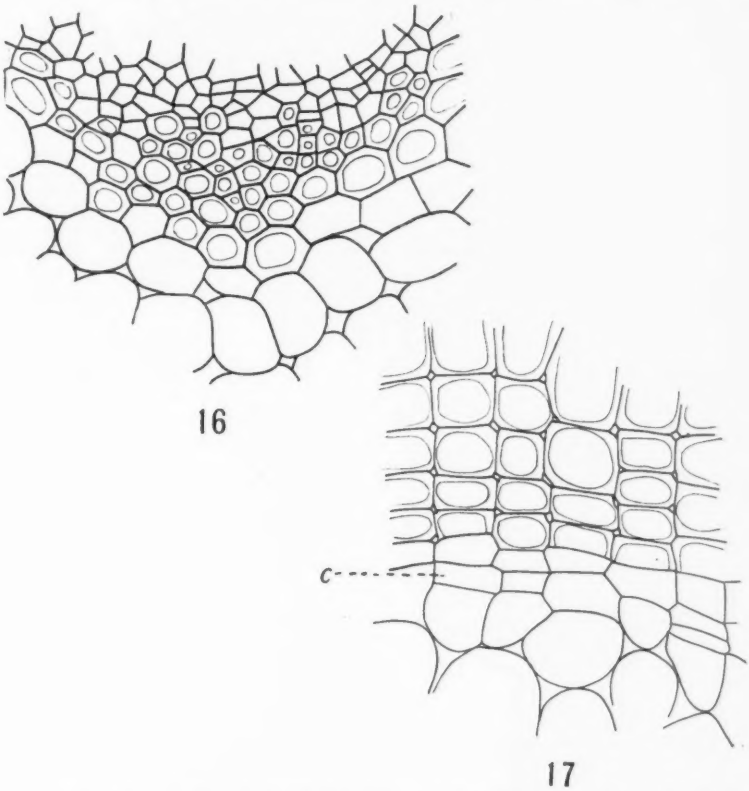
FIGS. 13–15.—Fig. 13, young stem of *P. methysticum* after differentiation has been completed, ×80; fig. 14, petiole, ×101; fig. 15, sector of stem after interfascicular cambium has been developed, ×101.

Secondary activity in the stem

There are two methods by which the stem of *Piper methysticum* enlarges: (1) by active division of pith cells; (2) by cambail activity.

1. In the center of and at irregular intervals throughout the pith, groups of cells will divide actively throughout the internode.

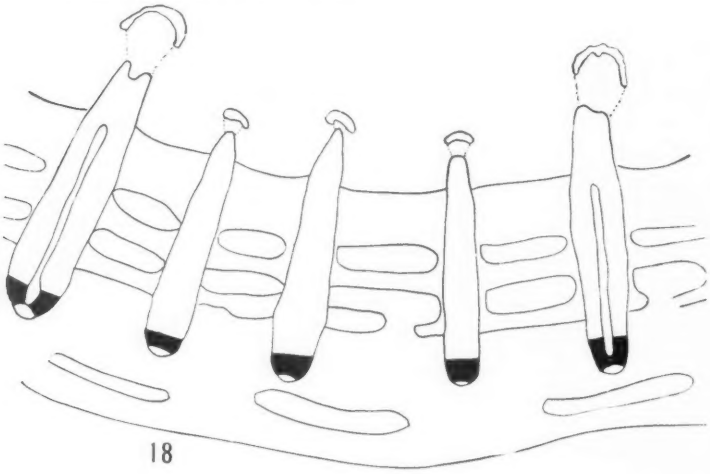
2. Each bundle of both the peripheral and pith rings has a cambium. The inner ones do not enlarge greatly. The outer or peripheral bundles lay down a ring of wood often 4–5 mm. in thickness. The proportion of xylem to phloem is about 8:1 (fig. 18).



FIGS. 16, 17.—Fig. 16, detail of pericycle of *P. methysticum;* fig. 17, detail of medullary ray; *C*, cambium; ×820.

Late in the history of the stem an interfascicular cambium appears (fig. 15), which cuts off segments on the inside only; very late a few segments may be cut off on the other side (fig. 17). This closes the stem cylinder. The interfascicular cambium appears much later in the nodes and remains active much longer.

VAN TIEGHEM calls attention to the one-sided action of the cambium in his work on *Piper nigrum*.



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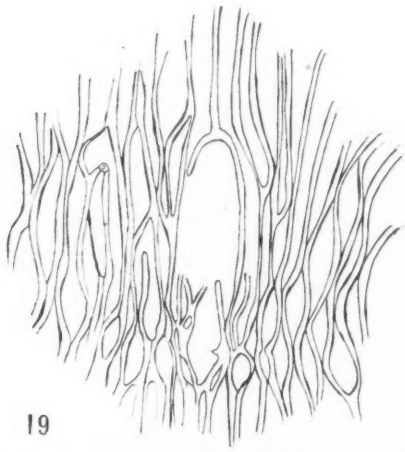

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FIGS. 18, 19.—Fig. 18, section of peripheral ring of the bundles of *P. methysticum* at a mature node, showing banded appearance of the rays, ×35; fig. 19, tangential section of peripheral bundles, showing branch gap; ×7.

The medullary ray becomes lignified and in longitudinal section shows pitted cells. At the node in the largest stems avail-

able, cells next to the cambium do not lignify and remain active. These are also scattered at irregular intervals throughout the ray. In section this gives the ray an irregular banded appearance (fig. 18). There are no growth rings. Much of the wood parenchyma touching the pith retains its activity at the node and divides long after secondary wood has been laid down. This pushes the primary vessels of the bundles apart at great distances, as well as the cells of mechanical tissue (fig. 18).

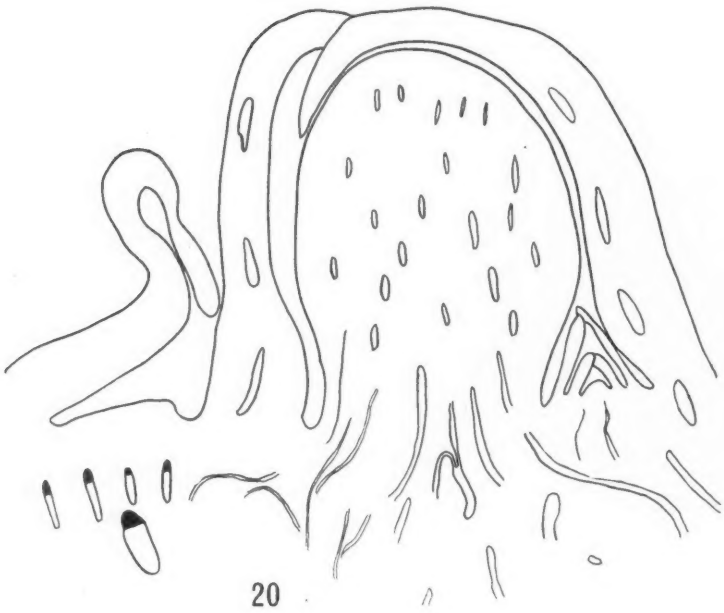
The stem when young is packed with starch and piperin. Mucilage cells are scattered throughout it, and the buds especially are covered with mucilage.

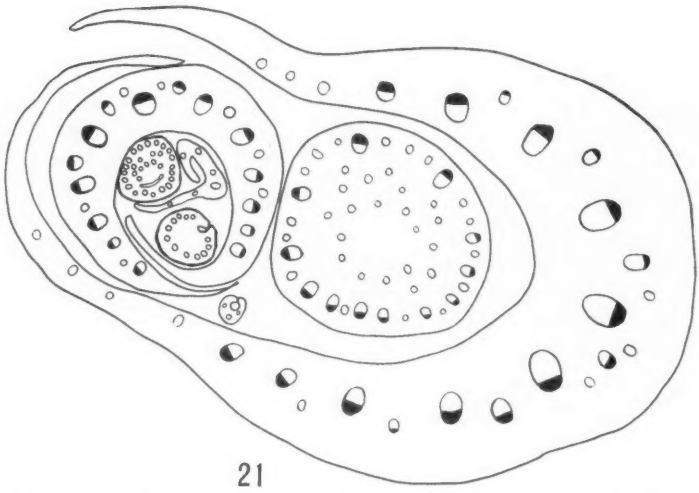
Leaves

The leaves have distinct petioles, the sheathing bases of which extend entirely around the stem, which becomes narrow opposite the point of insertion of the leaf. The leaf traces vary in number from 7 to 14. The bundles may be of two sizes. The lower part of the petiole is flattened on one side; the upper part is circular. The bundles form a crescent in the lower portion of the petiole (fig. 21), this crescent being made complete in the upper portion by the branching of the bundles at the points of the crescent (fig. 14). The secondary bundles form a more or less complete outer ring, are of the same type as those of the stem, and anastomose at any portion of the petiole. Union of the primary and secondary bundles, however, takes place before the traces enter the blade, which has 7–9 strong palmate veins, the 3 median ones running parallel for a while before they swing out laterally. The vernation of the leaf is involute.

Branching

Buds are borne in the bases of the sheathing petiole, the number varying from 1 to 3. The appearance of a single bud is often to one side instead of in the median position, which probably accounts for the appearance of branches coming from the side of the leaf. The buds are invested by a large amount of mucilage. The central bundles of the branch connect with those of the stem, and the peripheral ones connect with the peripheral bundles of the





FIGS. 20, 21.—Fig. 20, transverse section of mature and young buds, ×32; fig. 21, transverse section through the base of a petiole, showing branches arising in axils of abortive leaves, ×28.

stem (fig. 20). In two cases it was observed that the branch did not develop in the axil of a leaf where only the blade was developed (fig. 21), which was due probably to the pressure caused by the enveloping sheaths of the preceding leaves.

Piper umbellatum

The stem of *Piper umbellatum* is not essentially different from that of *Piper methysticum*. At maturity it has only one ring of pith bundles. The bundles, instead of traversing two nodes as internal bundles before fusing with the next group, traverse but one (fig. 22). The young plants are covered with hairs, both unicellular and multicellular. The number of leaf traces is 7–9. In the young stem there is an abundance of mucilage scattered in all regions. In the old stem a single mucilage canal appears in the center, which is continuous through the nodes and in the branches; VAN TIEGHEM found none that was continuous through the nodes (fig. 23).

Summary

1. The stem of *Piper methysticum* consists of two systems of bundles, peripheral and pith, the latter being in two rows.

2. The peripheral bundles are of two sizes: primary, the larger; secondary, the smaller. The latter are branches of the former.

3. The bundle type is collateral endarch.

4. The bundles are of foliar origin.

5. The bundles, after entering the stem, remain in the peripheral region through one internode and then traverse the pith for two internodes.

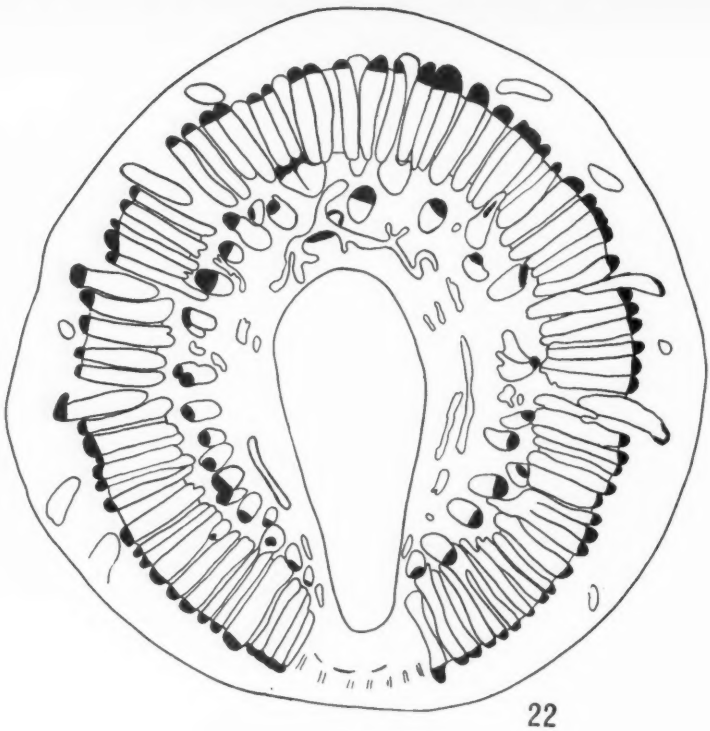
6. Both the peripheral and pith bundles show anastomoses.

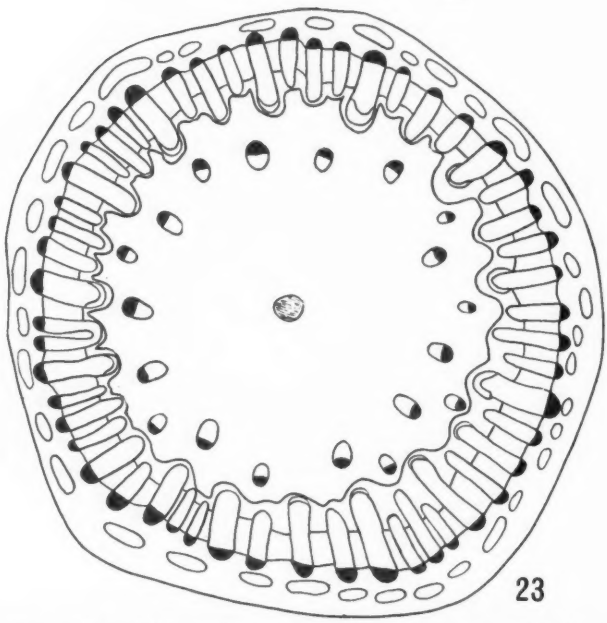
7. The pericycle consists of only a few cells outside the bundles, which become lignified.

8. There is no differentiated endodermis.

9. The stem enlarges by cambial activity and divisions in the pith region.

10. An interfascicular cambium appears late in the internode and cuts off segments only on one side; it comes still later in the nodes.





FIGS. 22, 23.—*P. umbellatum:* fig. 22, section through mature node; fig. 23, section through internode; ×12.

11. Leaf traces are many.

12. The base of the leaf is sheathing and vernation is involute.

13. Buds vary in number and position.

14. *Piper umbellatum* differs from *Piper methysticum* in the following ways: (1) one ring of pith bundles only; (2) the mucilage canal runs through the center of stem and node; (3) the bundles run through one internode only in the periphery and one in the pith before fusing with those of the leaf above.

15. Both stems are packed, especially when young, with starch, piperin, and mucilage.

16. There are no growth rings.

Discussion and conclusions

The anatomy of *Piper methysticum* and of *Piper umbellatum* agree for the most part with the anatomy of the species of *Piper* already described; especially is this true in reference to the work of DE BRAY (**3**; see also DE BARY **2**). VAN TIEGHEM reports a differentiated endodermis in all species of *Piper*, but this was lacking in these forms.

The question of most importance is the relationship shown by these forms. SINNOTT and BAILEY (**13, 14**) assert that the most primitive condition of angiosperms was woody, and that there is a tendency toward the herbaceous habit in the more recent groups. These forms show a tendency toward elimination of secondary growth and a breaking up of the woody cylinder in the following characters: (1) the pericycle is broken and all that remains is a small patch outside of each bundle; (2) the interfascicular cambium appears late in the internode and still later in the nodes; when it does occur the activity is primarily on one side; (3) there is a tendency toward the scattering of the bundles in the pith. These, together with the sheathing base of the petiole, the multilacunar (SINNOTT **13**) type of node, and the anastomosing of the bundles at the side, show a monocotyledonous tendency. Moreover, the embryo sac of the group shows the elimination of one division in oogenesis.

One may conclude from this combination of characteristics that *Piper methysticum* and *Piper umbellatum* lie in a group well

toward the level of monocotyledons, and the conclusion is borne out by the female gametophyte.

The writer is indebted to Professor JOHN M. COULTER for suggestions and criticisms, and to Dr. W. J. G. LAND for the material used and for direction and encouragement during the investigation.

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THE STRUCTURE OF THE BORDERED PITS OF CONIFERS AND ITS BEARING UPON THE TENSION HYPOTHESIS OF THE ASCENT OF SAP IN PLANTS

IRVING W. BAILEY

(WITH PLATE I AND TWO FIGURES)

The structure and the function of bordered pits have been studied by a number of investigators, particularly in connection with various well known theories in regard to the "ascent of sap" in plants. The consensus of opinion among botanists[1] seems to be that these complex pits are valvelike structures which facilitate the flow of water from the lumen of one tracheid or vessel into those of the adjoining ones. By means of the embossed areas of the secondary walls, a comparatively large surface of the delicate permeable membrane is exposed without seriously impairing the strength of the cell (text fig. 1). The torus or central thickened portion of the membrane acts as a valve, which may be deflected from its median position until it rests over one of the openings in the secondary walls (figs. 2, 3). In this way the delicate, permeable membrane is prevented from being ruptured when excessive pressure is brought to bear upon it. Furthermore, it has been generally admitted by anatomists and physiologists that the membranes of the bordered pits in conifers form complete septa that are impervious to finely divided solids and undissolved gases.

STRASBURGER suggested, accordingly, that the bordered pits functioned, in the ascent of the sap, as filters for preventing the penetration of air into the water-conducting elements. This view is also held by DIXON,[2] who states: "Thus, from the point of view of the tension hypothesis, we regard the bordered pits as mechanisms to render the walls as permeable as possible to continuous water

[1] See ELFVING, SCHWENDENER, PAPPENHEIM, RUSSOW, HARTIG, SCHACHT, DIPPEL, SANIO, DE BARY, STRASBURGER, EWART, DIXON, and others.

[2] DIXON, H. H., Transpiration and the ascent of sap in plants. London: Macmillan. 1915 (p. 99).

streams, while, when conditions require, they provide, by an automatic change, a rigid support to the tensile sap and oppose an impermeable barrier to undissolved gas."

In studying the fundamental factors which control the penetration of preservatives into green and seasoned timber, the writer[3]

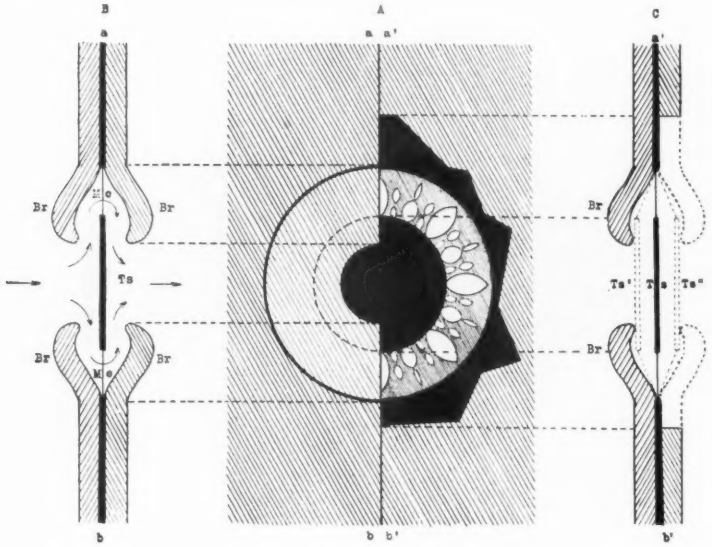

FIG 1.—*A*, piece of radial wall of a tracheid, showing a bordered pit in surface view; on the left, part of the dark colored *torus*, or thickened portion of pit membrane, may be seen through the *oriface* in the *embossed* secondary wall; on the right, part of this overlying wall has been removed, exposing a surface view of the *torus* and *perforated membrane; B*, view of section *a–b* through bordered pit, showing *embossed overlying and underlying secondary walls* (*Br*), *torus* (*Ts*), and *membrane* (*Me*); *C*, view of section *a'–b'*, showing how the torus acts as a *valve* by taking the positions *Ts'* or *Ts''*.

has had occasion to analyze critically the data upon which these conclusions in regard to the structure and function of the pit membranes are based.

[3] BAILEY, I. W., The validity of certain theories concerning the penetration of gases and preservatives into seasoned wood. For. Quart. 11:5–11. 1913.

———, The structure of the pit membranes in the tracheids of conifers, and its relation to the penetration of gases, liquids, and finely divided solids into green and seasoned wood. For. Quart. 11:12–20. 1913.

The experimental evidence, which has been considered to demonstrate that the pit membranes are unperforated, consists of injection experiments, such as the well known tests of SACHS with mercury and powdered cinnabar. That absence of penetration in these experiments may have been due to other factors than the unperforated character of the pit membranes does not appear to have suggested itself to previous investigators. However, there are two possibilities that should be emphasized in this connection. In the first place, it is hardly to be expected, a priori, that mercury, alloys of low melting points, and similar substances should penetrate the pit membranes, even if they were porous or sievelike in structure. Owing to the small size of the tracheids and bordered pits in conifers, and the valvelike action of the tori, the very high surface tensions of heavy liquids would tend to prevent their penetration. In the second place, the structure of coniferous wood, particularly that of *Taxus*, is such that injection masses containing finely divided particles (for example, gamboge, India ink, cinnabar, etc.) would be very likely to clog the pits or to deflect the tori before they could succeed in passing through the minute openings in the pit membranes. This would be true even if the particles were considerably smaller than the perforations in the membranes, and is well illustrated by the frequent failure of India ink to penetrate the narrow cavities of "summer" tracheids when portions of the walls of the latter have been cut away.

In selecting an injection mass, therefore, it is very essential that its surface tension and viscosity should be similar to that of the sap in trees, and, if it contains a finely divided solid, the particles of the latter should be of such a size and in such numbers that clogging and deflection of the tori are reduced to a minimum.

That the failure of various investigators to secure penetration with suspensions may have been due to clogging rather than to the unperforated character of the pit membranes was suggested by the following experiments. Pieces of the wood of various conifers were immersed in India ink and subjected alternately to pressures of +10 and −10 lbs. In this way the tori were continually deflected from side to side to facilitate penetration. Figs. 1 and 4 show the dark colored injection mass passing from one tracheid into an adjacent one through the bordered pits.

Of course, the objection may be raised that the membranes were ruptured by the process of injection. This seems to be highly improbable, however, since in a special series of experiments, devised for the purpose, the writer was unable to rupture the membranes, even under a pressure of 250 lbs. per square inch. In order to obviate this difficulty entirely, the India ink was much diluted with distilled water, and allowed to percolate through sticks of freshly cut sap wood[4] under slight hydrostatic pressure (0.25 oz.). Under these conditions the India ink[5] passed through the bordered pits easily and rapidly.

By experimenting with various methods of cutting, staining, and mounting sections, the writer finally succeeded in making visible and photographing openings in the membranes (fig. 6) of the pits of *Larix laricina*. The reason that the perforations have escaped observation is undoubtedly due to the fact that the pit membranes are extremely minute and attenuated, and their structure is obscured by the thick overlying walls. Unless the embossed portions of the secondary walls are cut away, leaving the membranes exposed and uninjured, a somewhat difficult undertaking, or a necessary combination of light refraction phenomena is secured, the perforations remain invisible.

It should be noted in passing that a perforated structure of the pit membranes makes possible an entirely different interpretation of the penetration of gelatine, paraffin, cacao butter, and similar substances into the xylem of conifers. In discussing SACHS' imbibition hypothesis and the mobility of water in tracheid walls, the significance of ELFVING'S experiments with cacao butter and those of ERRERA and STRASBURGER with gelatine has been questioned upon the assumption that, because cacao butter and

[4] Tests made with *Pinus Strobus* L., *P. rigida* Mill., *Picea rubra* (DuRoi) Dietr., *Larix laricina* (DuRoi) Koch., *Tsuga canadensis* (L.) Carr., *Juniperus virginiana* L., and *Taxus cuspidata* Sieb. and Zucc.

[5] The various commercial India inks vary considerably in the size of the carbon particles of which they are composed. Although the writer has succeeded in securing penetration with various Asiatic inks, they are usually composed of too coarse particles, and tend to clog quickly. Higgins' India ink contains much smaller and more uniform carbon particles and gives much easier and rapid penetration. In using India inks as injection masses the writer has been careful to make sure that that portion of the ink which passed through the membranes contained visible particles of carbon.

gelatine pass through the septa of the bordered pits, the walls of the tracheids must absorb them. In view of the perforated structure of the pit membranes in larch and in other conifers, and JÖNSSON's observations upon the sievelike membranes in the vessels of angiosperms, these criticisms of the work of ELFVING, ERRERA, and STRASBURGER do not appear to be entirely conclusive.

The presence of bubbles of undissolved gas in the wood of transpiring plants has been considered to be a serious objection to the cohesion hypothesis of the ascent of sap in plants; for it has been admitted by DIXON (*l.c.*) that a bubble, having a diameter of 0.02 mm. or more, would destroy the possibility of tension in any tracheid or vessel which is located more than a few feet from the ground. DIXON avoids this difficulty by stating that, although there is undoubtedly considerable undissolved air or gas in the sap wood of plants, not all of the tracheids or conducting elements contain bubbles; that is, a large number of tracheids may be blocked by air, yet all the continuous water columns in the wood need not be broken (text fig. 2). This is considered to be due to the fact that the membranes of the bordered pits prevent undissolved gas from passing from one element into adjoining ones.

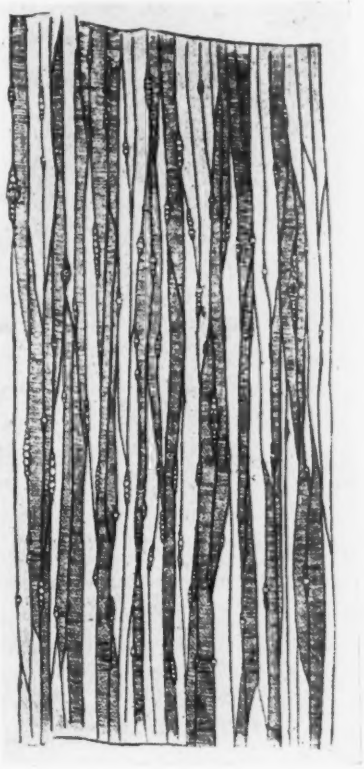

FIG 2.—Longitudinal tangential section of coniferous wood, showing continuous water columns in spite of the fact that nearly half of the tracheids are filled with air; after DIXON.

It is evident, therefore, that in a discussion of the tension hypothesis, the porous or sievelike structure of the pit membranes of conifers deserves careful consideration.

It has been estimated by DIXON (*l.c.*) that "the tension applied to the upper end of water columns, which will be able to raise the transpiration stream in a tree, must equal the pressure produced by a head of water twice the height of the tree." In trees 75–300 feet in height, therefore, there must be forces of 5–20 atmospheres, tending to draw air and other gases, through the perforations in the pit membranes, into the water-conducting passageways. This raises the question: Are the perforations in the membranes of such small size that the surface tension of the sap in them will be great enough to resist the penetration of gas under forces of 5–20 atmospheres?

Perforations of different shapes and sizes occur in each pit membrane (text fig. 1 and fig. 6). The larger openings generally are more or less elongated in outline, but many of the smaller ones are oval or circular. In the stem wood of *Larix laricina* the average diameter of the openings was found to vary somewhat as follows: largest perforations, 3.0 μ; medium perforations, 1.6 μ; small perforations, 0.5 μ.

In calculating the surface tension of liquids in circular openings, the expression of CANTOR[6] is commonly used. This is as follows:

$$y=\frac{rH}{2}-\tfrac{1}{3}\,dr^2-\frac{d^2r^2}{2H},$$

in which y = surface tension in dynes, r = radius of hole in centimeters, H = air pressure in dynes per square centimeter, and d = density of liquid. Assuming a temperature of 15° C., and that the pressure of one atmosphere equals 1,013,000 dynes, the pressure needed to overcome the surface tension of water in circular perforations of the foregoing diameters should be as follows: small perforations, 5.8 atmospheres; medium perforations, 1.8 atmospheres; large perforations, 1.0 atmosphere.

That the actual pressures required to overcome the surface tension of sap in the perforations of the pit membranes would differ

[6] Wied. Ann. **47**:399. 1892.

from these figures seemed probable, since sap is not pure water, the membranes are elastic, the openings are not perfectly circular in most cases, and the formula is of questionable value in dealing with holes of such minute radii.

In order to check the matter experimentally, a series of tests were made to determine what pressure is required to force air through the membranes of conifers when they are saturated with sap, distilled water, glycerine, acetic acid, acetone, ethyl alcohol, and other liquids of varying surface tensions. A hemlock (*Tsuga canadensis*) 85 feet and a larch (*Larix laricina*) 60 feet in height were felled, and pieces of sap wood including the last formed layers were removed at various points along the stem. These specimens were cut (under water) into small cylinders and carefully tested to determine the location of tracheids which contained bubbles of air or gas. Microscopic examination of the material showed that, at the season when the wood was cut (November), very few of the tracheids of the last formed layers of growth of hemlock and larch contained bubbles of air or gas. Those tracheids which contained gas were conspicuous, owing to their lighter color, and their presence could be demonstrated, in cylinders of sap wood used for experimental purposes, by allowing a dilute solution of India ink to pass through the specimens. The ink traveled very rapidly in those elements that were filled with water, and comparatively slowly, or not at all, in cells which contained bubbles of gas.

In determining the pressures required to overcome the surface tension of the liquids in the perforations of the pit membranes, those pressures were recorded at which air succeeded in penetrating all of the water-filled tracheids.[7] As might be expected from the variation in the size of the perforations, the air penetrated many tracheids before these pressures were attained.

After testing a specimen with alcohol, acetic acid, acetone, etc., it was washed clean, thoroughly re-soaked with distilled water, and retested in order to determine whether the membranes had remained unaffected by the liquids.

[7] That the air which passed through the specimens did not travel in intercellular spaces was determined in two ways: by direct observation with a binocular microscope, and by the fact that the lumens of the tracheids, which at the beginning of the tests were filled with liquid, contained air at the end of the experiments.

The following values are representative of many secured for hemlock, the specimen of sap wood being taken 75 feet from the ground.

Pressure required to force air through tracheids filled with—

1. Sap..... 30–40 lbs.
2. Distilled water..... 30–40 "
3. Glacial acetic acid..... 12–16 "
4. Distilled water..... 30–40 "
5. Ethyl alcohol 99+percentage..... 6–10 "
6. Distilled water..... 30–40 "

These figures indicate that the values obtained by the use of CANTOR'S equation are in all probability somewhat in excess of the actual values for the irregular openings in the elastic membranes of conifers; for the perforations in hemlock are considerably smaller than those which occur in larch, and in forcing air through the tracheids, other resistances, besides that of the surface tension of sap in the openings of the membranes, have to be neutralized.

In all of the specimens tested by the writer, which included sap wood of various pines and spruces, as well as larch and hemlock, the surface tension of the sap in the pit membranes could be overcome by air pressures of less than 3 atmospheres. In passing up the stem of a tall tree, the pressures required to overcome the surface tension of sap in the pit membranes do not appear to vary considerably in wood removed at similar distances from the pith.[8] On the other hand, the tension in the sap, according to the cohesion hypothesis, increases very rapidly. It is evident, accordingly, that in tall trees the forces tending to pull gas through the perforations in the pit membranes will greatly exceed the surface tension of the sap in the pores of the membranes. Furthermore, it is significant that in *Sequoia*, many specimens of which exceed 300 feet in height, the perforations are larger than they are in such small conifers as *Taxus*, *Juniperus*, *Pinus edulis*, etc.

In order to determine whether the valvelike action of the tori may be effective in sealing the pits and preventing the penetration

[8] Through the courtesy of various members of the U.S. Forest Service, I have been able to secure pieces of *Sequoia* that were cut from the tops of trees over 200 ft. in height.

of gas, under forces of considerable magnitude, air pressures of 50–200 lbs. were applied to various conifers. The air passed through the membranes in all cases, whether the pressures were gradually or suddenly applied.

Summary and conclusions

Exception is taken to statements that the membranes in the bordered pits of conifers form complete septa that are entirely impervious to finely divided solids and undissolved gases.

Perforated pit membranes are clearly visible in properly stained sections of *Larix* and *Sequoia*. Owing to the minute size and tenuity of pit membranes, their detailed structure is more or less obscured by the thick, overhanging secondary walls.

Aqueous solutions, containing finely divided particles of carbon, can be made to pass through the membranes in the bordered pits of sap wood taken from the stems of large specimens of *Larix*, *Sequoia*, and other conifers.

The presence of perforations in the membranes is also indicated by the fact that large quantities of gases can be forced rapidly through the bordered pits of tracheids that are thoroughly saturated with sap.

The surface tension of sap in the pit of membranes of various conifers can be overcome by pressures of less than 3 atmospheres.

The tension hypothesis of the ascent of sap in plants, as interpreted by DIXON, requires continuous columns of water, which, at the tops of trees, 75–300 ft. in height, are subjected to tensions of 5–20 atmospheres. In other words, the bordered pits must be impervious to undissolved gases under pressures of 5–20 atmospheres.

It remains to be shown how continuous columns of water can be maintained in tall conifers when the membranes in the bordered pits may become permeable to undissolved gases at pressures of less than 3 atmospheres.

In conclusion, the writer wishes to express his sincere thanks to various members of the United States Forest Service, Mr. R. D. SWALES of the Union Lumber Company, and the Director of the

Harvard Forest for material of conifers, and to his colleagues, Professors T. W. RICHARDS, P. W. BRIDGMAN, and Dr. W. T. BOVIE for helpful suggestions.

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EXPLANATION OF PLATE I

FIG. 1.—*Pinus Strobus* L.: tangential section showing penetration of carbon suspension through bordered pits of freshly cut sap wood; ×700.

FIG. 2.—*Pinus* sp.: tangential section through bordered pit showing torus jammed into opening in secondary wall of left-hand tracheid; ×1000.

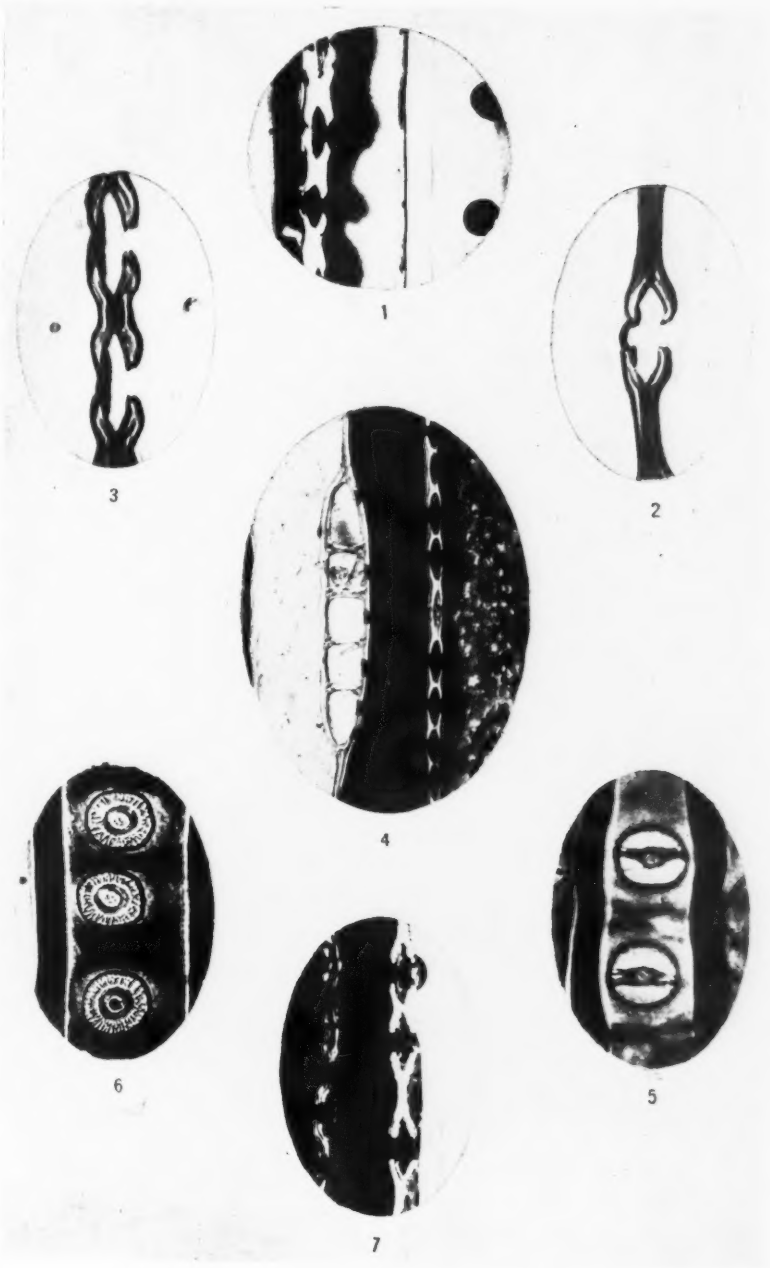
FIG. 3.—*Pinus* sp.: tangential section through 2 bordered pits showing usual valvelike action of tori; ×1000.

FIG. 4.—*Sequoia sempervirens* Endl.; tangential section showing penetration of carbon suspension through bordered pits; ×300.

FIG. 5.—*Dacrydium Franklinii* Hood: radial section showing peculiar strap-shaped tori; ×700.

FIG. 6.—*Larix laricina* (DuRoi) Koch: radial section showing perforations in pit membranes; ×520.

FIG. 7.—*Pinus palustris* Mill.: tangential section showing heavy tar oil passing through bordered pits; ×600.



BAILEY on BORDERED PITS

AVEN NELSON AND J. FRANCIS MACBRIDE

Plagiobothrys Harknessii (Greene), n. comb.—*Sonnea Harknessii* Greene, Pitt. **1**: 23. 1887.—Quite distinct from *P. Kingii*, its nearest relative, as GREENE has well shown (*l.c.*). The following representative collections indicate that its range is much greater than originally supposed. NEVADA: Eagle Valley, Ormsby County, June 10, 1902, *C. F. Baker* (1046); CALIFORNIA: Sierra County, 1875, *J. G. Lemmon* (794); OREGON: near Desert Well, 8 miles south of Big Springs, July 5, 1894, *J. B. Leiberg* (403).

Plagiobothrys foliaceus (Greene), n. comb.—*Sonnea foliacea* Greene, Pitt. **1**: 222. 1888.—This seems to be a well marked species, the dorsal depression of the nutlets being particularly unique, but it is apparently still known only from the original collection.

The maintenance of *Sonnea* Greene (*l.c.* 22) does not seem to be at all desirable. Although, as pointed out by GREENE, the character of the scar in this group is somewhat different from that of the other species of *Plagiobothrys*, the plants are habitally the same when one takes the genus into consideration in its entirety. Moreover, the scar character is not so characteristic in all the species as might be desired if they are to be removed from true *Plagiobothrys*. In this connection JONES has called attention to the fact that *P. Jonesii* (*S. Jonesii* [Gray] Greene) is an *Amsinckia* in everything but its white flowers (Contrib. West. Bot. **12**: 57. 1908). The pubescence of *P. Jonesii* and the tesellated nutlets surely suggest a relationship to *A. tessellata*, but the white and short corollas that are so widely at variance with the long yellow ones of *Amsinckia* are perfectly congeneric with the SONNEA section of *Plagiobothrys*. Altogether, *Sonnea* would seem superfluous in a group of genera already merging, but which, with *Sonnea* eliminated, seem well enough marked when dealt with in their aggregates.

Cryptantha vinctens, n. sp.—Annual, 10–15 cm. high, rather sparsely pilose or hispidulous, the leaves more or less papillose;

leaves essentially oblong, 1–2 cm. long, 2–3 mm. broad: inflorescence about 1 cm. long, peduncled, terminating the main stem and its lateral branches, mostly 2-forked, close even in age: corollas minute: calyx persistent and often in fruit very finely appressed-hispid, without a lens appearing silky; sepals ovate-lanceolate, 2.5–3.5 mm. long, the midrib pronounced but not cartilaginous: nutlets 3–4, nearly 2.5 mm. long, mainly ovate, lustrous brown, or gray-spotted with brown, very smooth, acutely angled, but not margined; groove closed or slightly open near the forked and closed base.

Rocky slopes Malheur Valley, near Harper Ranch, Oregon, alt. 1100 ft., June 10, 1896, *J. B. Leiberg* 2235 (type in Gray Herb.).

This specimen was distributed as *C. submollis* (Gray) Coville (*C. utahensis* [Gray] Greene), and that species is its nearest ally. However, the perfectly smooth, less sharply angled nutlets, with closed or nearly closed groove, and the larger sepals are some of the characters which forbid its being referred to *C. utahensis*. The larger calyces suggest *C. mohavensis* Greene, but in that species and in its near relative *C. oxygona* (Gray) Greene the flowers are conspicuous and the nutlets broader and acutely margined. *C. vinctens* and *C. utahensis* occupy positions analogous to those of *C. mohavensis* and *C. oxygona*, except that the two former are more distinct from each other than are the two latter. Furthermore, *C. vinctens* and *C. Bartolomaei* Greene (the only other member of the group) are (as pointed out by GREENE in regard to his species) connecting links between the smooth-fruited species in the deciduous calyx and persistent calyx groups. *C. Bartolomaei* is apparently confined to Lower California, and there it is unique in its pubescence and minute nutlets. None of the species, except *C. vinctens*, has been secured farther north than Utah or Nevada, the distribution of the group apparently centering in the desert areas of the southwest.

Oreocarya dura, n. sp.—Perennial, the single caudex densely clothed with leaf bases of many years: stems usually single, 1–1.5 dm. high, strigillose and densely hispid with widely spreading hairs: leaves oblanceolate or nearly oblong, about 3 cm. long and 5 mm. wide, not greatly reduced on the stem except in the inflorescence and there bractlike, densely shaggy with an indument of fine tangled hairs almost concealed by numerous pustulate-based spreading hirsute hairs: inflorescence a thrysoid glomerule: calyx densely hispid with greenish yellow hairs, the linear divisions about 4.5 mm. long, a little longer than the corolla tube: corolla white; appendages prominent: fruit unknown.

Although it is not possible to state definitely the relationship of this plant, since the fruit is not known, it is probably nearest those species characterized by muriculate not at all rugose nutlets, such as *O. Shantzii* and *O. nana*. However, its shaggy pubescence and simple perennial caudex mark it as distinct from any species of the short corolla section of the genus. The type, in the Rocky Mt. Herb., is *E. T. Johnson* 418, 1907, Central Colorado.

Oreocarya propria, n. sp.—Cespitose perennial: branches of the woody caudex densely clothed with the bases of past seasons' leaves: leaves numerous, 3–6.5 cm. long, half of this length gradually narrowed from the spatulate blade portion into a petiole which abruptly widens into a fibrosely woolly base; stem leaves mostly much reduced and bractlike; pubescence very appressed, finely strigose, on the upper leaf surfaces, also sparsely hispid, the appressed hispid hairs inconspicuously pustulate at base: stems 1–2 dm. high, floriferous above the basal leaves: inflorescence spikelike, consisting of axillary racemes or clusters, the lower often reduced to a single flower in a leaf axil: calyces on distinct pedicels, strigose and densely covered with spreading yellowish bristles; divisions linear, open in fruit, 3–5 mm. long: corolla white, the tube very slightly exceeding the calyx: nutlets ovate, 3–4 mm. long, evenly roughened with very fine intersecting and sinuous ridges, so as to appear irregularly foveolate; ventral groove enlarging toward the base.

This species is most closely related to *O. nana* Eastw. It is very distinct, however, in its racemose inflorescence, with different pubescence. The old leaves are covered with argillaceous soil in which the plant grew. OREGON: Vale, Malheur County, May 14, 1896, *J. B. Leiberg* 2049 (type in Gray Herb.); chalky hillsides, Malheur Valley, near Harper Ranch, June 8, 1896, *J. B. Leiberg* 2223.

Amsinckia carinata, n. sp.—Foliage, pubescence, calyx, corolla, etc., of *A. vernicosa* H. and A.: nutlets lustrous, smooth, very dark gray with a few darker markings, not less than 5 mm. long, not at all triquetrous, the angles obtuse (almost rounded), the back somewhat concave but distinctly carinate by reason of a raised but rounded ridge; ventral surface sharply keeled, the acute edge, including the linear scar, ending abruptly near the base where there are two distinct depressions, giving the impression of an open bifurcation.

OREGON: rocky soil, Malheur Valley, near Harper Ranch, alt. 1100 ft., June 10, 1896, *J. B. Leiberg* 2234 (type in Gray Herb.). It is surprising indeed to find a representative of this alliance so far north. *A. grandiflora* Kleeb, the species which *A. carinata* so closely simulates in habit, has not been collected north of San Francisco or Monterey. The Oregon species does not seem to differ from *A. vernicosa* except in its fruit; it is only related to *A. grandiflora* in a general way; its nutlets are radically different from both. Mature nutlets of *A. vernicosa* are bright gray, speckled with black, 4–4.5 mm. long, sharply triquetrous (like monster buckwheat grains), and with no obvious scar.

Mertensia Palmeri, n. sp.—Apparently tufted on a woody root: stems ascending, 2–3 dm. high, ciliate-hirsute: leaves ciliate-hirsute below, minutely hispid above; radical leaves ovate, obtusish, 2–5 cm. long, on stout petioles somewhat shorter; stem leaves broadly ovate, 5–10 cm. long, cuneately tapering to the acute apex, the stout margined petioles very short: inflorescence appressed-strigose, paniculate, few-flowered: calyx cleft to the base; the sepals linear-lanceolate, 6–7 mm. long: corolla with broad tube only as long as the calyx, the limb with rather strongly dilated throat and nearly 1 cm. long.

The type was collected somewhere in Arizona by *E. Palmer*, 1869 (no other data). It was distributed as *M. paniculata* Don.? It is deposited in the National Herbarium, the sheet bearing the accession no. 46975, and apparently is related to *M. pratensis*, but is remarkable because of the hirsute stems.

TETRACLEA COULTERI Gray, var. angustifolia (Wooton and Standley), n. comb.—*Tetraclea angustifolia* Wooton and Standley, Contrib. Nat. Herb. **16**:170. 1913.—Usually readily distinguished from the species by the narrowly oblong leaves. *T. Coulteri* varies in leaf shape considerably, however, and its leaves are often as strongly toothed as are those of the variety. The narrow leaved plants exhibit no other differences that are worthy of note and that may not be found in any representative series of the species.

At present known only from southern New Mexico, by *E. O. Wooton* (*l.c.*); and more recently by *A. Davidson*, of Los Angeles, who secured specimens at Summit, October 1, 1900, no. 352*a*, and at Duncan, September 1, 1902, no. 1078.

A new section of Pentstemon

In BOT. GAZ. **55**: 381. 1913 we published a species of *Pentstemon* (*P. rex*) in which the anther cells remain closed and saccate at the apex. As stated there, this character seems to have been noted

heretofore only in the red-flowered group, some of which have the anther cell saccate at base and some at apex. It is interesting, therefore, to find two more very distinct species having this unusual anther structure. It is of further interest that, so far, all the species of the section or subsection are from Idaho and have been evolved under similar environments.

The three species may be discriminated as follows:

Herbage more or less puberulent; corolla large (3–4 cm. long); sterile filament glabrous or nearly so ..... *P. rex*
Herbage glabrous; sterile filament bearded
Flowers about 12 mm. long, in a dense slender thyrse ..... *P. minidokanus*
Flowers about 18 mm. long, few, subsessile in axils of linear bracts *P. payetensis*

Pentstemon minidokanus, n. sp.—Glabrous throughout, pale: stems slender, 3–5 dm. high: basal leaves narrowly oblanceolate; stem leaves linear-oblong, passing into linear-lanceolate upward: flowers in a long narrow more or less drooping thyrse, deep blue, small for the *P. rex* section: corolla only 12–15 mm. long, gradually dilated, glabrous within and without: sepals ovate, acute, purplish, about 3 mm. long: anthers cells rather short and thick, not explanate, dehiscent from the base to a closed saccate apical portion of about one-fourth their length; sterile filament moderately bearded at the apex.

Based on specimens secured in the Minidoka, Idaho, National Forest, by *Geo. D. Crockett* of the Forest Service, July 17, 1913 (type in Rocky Mt. Herb.).

Pentstemon payetensis, n. sp.—Glabrous throughout, 3–5 dm. high: leaves rather few and remote; the basal lance-oblong, 4–6 cm. long, on slender petioles more than half as long; the cauline oblong, acuminate, passing into the linear bracts: flowers few, subsessile in the subsessile axillary cymes: sepals 6–9 mm. long, the very slender acumination about twice as long as the ovate oblong body: corolla blue, 20 mm. or less long, its tube about half as long as the moderately dilated limb, glabrous: anther cells as in the preceding; sterile filament scarcely dilated, sparsely bearded toward the apex with strongly refracted hairs.

Communicated to the Rocky Mt. Herb. by *G. B. Mains*, Supervisor of the Payette National Forest, being no. D-73 of the collection in the Supervisor's office at Payette; type in Rocky Mt. Herb. bearing accession no. 72941.

Machaeranthera rhizomata, n. sp.—Perennial from such a running rootstock as is often seen in *Solidago* and *Aster*, with numerous slender roots: stem strict and simple, very leafy, 3–5 dm. high, minutely glandular with some scattered moniliform hairs: leaves quite entire, oblong-lanceolate to broadly linear, up to 3 cm. long, rather densely scabrous: heads few to several, in a short compact corymb with foliar bracts, scabrous-glandular especially on the involucres; involucral bracts linear-lanceolate with long dark-colored slender reflexed or refracted acuminations: rays linear: pappus sordid.

The rootstock, the entire leaves (the bristly tipped teeth wanting), the strict stem, and the compact terminal corymb readily distinguish this species. The type is *C. L. Shear* 3461, West Cliff, Colorado, August 13, 1896, and in the National Herbarium bears accession no. 835200.

Machaeranthera inops, n. sp.—A depauperate perennial, from a tap root, with few to several short widely divaricate or ascending stems from its crown: stems slender, simple or branched, 5–12 cm. long, densely canescent, as are also the leaves: leaves small, from obovate to spatulate-lanceolate, some of them crenately toothed around the summit: heads few, medium size; involucral bracts linear-oblong, subacute, minutely pubescent, obscurely or not at all glandular, some of the tips refracted: rays wanting: pappus fuscous.

The type sheet is no. 417219 in the National Herbarium, collected by *F. A. Walpole* on Glacier Mountain, Oregon, in the Crater Lake region, August 21, 1902, no. 2288.

MACHAERANTHERA INOPS Nels. and Macbr., var. **atrata,** n. var.—Closely resembling the species but with fewer stems and fewer, larger heads: involucres broadly turbinate rather than hemispheric, and bracts with dark-purple bands or margins.

Crater Lake Park, on firm pumice gravel at the summit of Llao Rock. It is *F. V. Coville* 1470, September 14, 1902. The type sheet bears no. 415285 in the National Herbarium.

Macronema filifomis, n. sp.—Low freely branched undershrub with the aspect of *Chrysothamnus*, 2–3 dm. high; herbage from glabrate to softly lanulose: leaves numerous, linear-filiform, 2–4 cm. long: heads numerous, paniculate, 8–10 mm. high, 10–15-flowered;

involucral bracts in 3 unequal series, linear-acuminate, with delicate membranous ciliolose margins: ray flowers few (1–4 or wanting), ligule oblong, 6–8 mm. long; disk flowers slender, tube longer than the slightly dilated throat: linear-acuminate anthers and stigmas well exserted: achenes brownish, softly pubescent becoming glabrate.

The material seen by the writers consists of two fine sheets collected by *F. V. Coville* and *Elmer I. Applegate*, under nos. 544 and 545, August 16, 1897 in *Pinus Murrayana* forest, on the headwaters of the Deschutes River, Crook County, Oregon. These are the type sheets and bear accession nos. 380795 and 380796 in the National Herbarium.

Macronema glomerata, n. sp.—Low undershrub, freely branched, whitened throughout with short dense woolly pubescence, 2–3 dm. high: leaves linear, 2–4 cm. long, 1–2 mm. broad, callous-tipped: heads few (4–10), crowded at the summit of the stems, 10–14 mm. high; involucral bracts unequal, resembling the leaves into which they pass: rays conspicuous, 2–5, linear-oblong; disk flowers about twice as many as the rays, their slender tubes longer than the fusiform throat: fuscous pappus about as long as the corollas: achenes silky, less than half as long as the pappus.

The splendid sheet of this species, accession no. 401293 in National Herbarium, is named as the type. It is *F. A. Walpole* 370, secured at Ashland, Oregon, September 12, 1899.

Macronema Walpoliana, n. sp.—An undershrub but probably taller than the preceding, the stems simple up to the narrow thyrsoid panicle of numerous heads, glabrate or with a minute lanate pubescence persisting in the inflorescence: leaves linear, subcuspidate, glabrate and subglutinous, 2–4 cm. long: involucre turbinate, its bracts scarious, sublanate or ciliate, in 2 or 3 series; number of flowers as in the last: rays with conspicuous oblong-linear ligules 10–14 mm. long: achenes brownish, sparsely pubescent, a little shorter than the copious fuscous pappus.

Distributed under *Aplopappus* without specific determination. From Klamath County, Oregon, *F. A. Walpole* 387 and 406, collected September 19 and 27, respectively, 1899. These two sheets bear accession nos. 401312 and 401334 in the National Herbarium, the latter being designated as the type.

Macronema scoparia, n. sp.—A profusely and fasciculately branched undershrub; the old stems with a grayish-brown shreddy

bark; the herbaceous stems slender, very leafy, greenish brown: leaves narrowly linear, glabrous and subglutinous, 1–3 cm. long: heads few, subracemose at the ends of the twigs; involucral bracts glabrous or obscurely ciliate on the scarious margins: rays none or only 1 or 2 in each head, the ligule oblong-linear and conspicuous; disk flowers not more than 5–8: the brown glabrous achenes not more than half as long as the pappus.

This was also secured by *Walpole* in Oregon. It bears his no. 386, Hunt's Ranch, Dead Indian Road, Jackson County, September 18, 1899. The type is on sheet no. 401311, National Herbarium.

Macronema pulvisculifera, n. sp.—Base evidently shrubby, the numerous branches 1–2 dm. high, naked below, very leafy toward the racemose-paniculate inflorescence, glabrous but covered with dustlike resinous or glandular particles even on the involucre: heads mostly terminal on the branchlets of the inflorescence, rather large (1 cm. or more), the narrowly linear foliar bracts passing into those of the involucre: rays conspicuous, 2–5, the ligule about 1 cm. long; disk flowers 10 or more, with slender achenes a little shorter than the pappus and slender corolla.

Based on a full sheet of specimens, no. 401010 in the National Herbarium collected by *F. A. Walpole*, on Mount Hood, Oregon, near Cloudleap Inn, no. 98, September 7, 1898.

Macronema imbricata, n. sp.—A pale green spreading shrub, glabrous but for a sparse glandular puberulence on leaves and involucres; main stems 2–3 dm. long, stout and prostrate, their numerous branches and the season's growth erect, about 1 dm. high, very leafy: leaves crowded and strongly overlapping, obovate-spatulate, the rounded apex tipped with a short tooth: heads solitary or very few at the ends of the branches, variable in size (7–12 mm. high); outer involucral bracts foliar, smaller but similar to the leaves with which they connect; inner bracts lanceolate, greenish with scarious margins: rays none, solitary, or very few, relatively short and broad; disk flowers many (15–25), the limb short and erect: achene brown, strigose, as long as the dingy pappus.

The type sheet is *Heller* 7182, "ridge south of Donner Pass, Nevada County, California, at about 8500 ft.," August 17, 1903. Deposited in the National Herbarium and bearing accession no. 467563. Originally distributed as *M. suffruticosa*.

CHAENACTIS MAINSIANA Nels. and Macbr. BOT. GAZ. **56**:478. 1913.—In the recent treatment of this genus in the *North American Flora*, the above species is reduced to *C. pumila* Greene (**34**:73. 1914). The latter is described as having the leaves "broadly obovate in outline," but in the key (*l.c.* 66) it is placed under the subdivision "leaves oblanceolate or ellipitic in outline." The subdivision parallel to this reads "leaves obovate cuneate or flabelliform in outline." Under this heading are placed *C. nevadensis* and *C. Evermannii*. The latter is scarcely more than a variety of the former, and in our publication we compared *C. Mainsiana* to these species, and according to the key referred to, it would have to be placed with these species because it has flabelliform leaves. But admitting that the key is fallacious (witness the disposition of *C. pumila*), let us compare *C. Mainsiana* with that species. *C. pumila* Greene, Leaflets **2**:221 (not 223 as in *North American Flora*) 1912, has "densely glandular-hirsute involucres" and "densely glandular peduncles" which are only 2–4 cm. long. These are characters which belong to *C. alpina* in greater or less degree, but are absolutely at variance with the characters of *C. Mainsiana*. The latter species, even when young, is greenish gray with a lepidote tomentum which is sprinkled with resinous atoms as in *Artemisia atomifera* Piper, and the peduncles, which usually bear more than one head, rise 5–10 cm. above the leaves. It is evident, therefore, that the nearest relative of this species is *C. nevadensis*, the species to which we originally compared it (*l.c.*); and it is very much more distinct from *C. nevadensis* than is *C. Evermannii* Greene, maintained in the *North American Flora*.

Evax breviflora (Gray), n. comb.—*E. caulescens* (Benth.) Gray, var. *brevifolia* Gray, Syn. Fl. **1**:229. 1888; *Hesperevax brevifolia* Greene, Fl. Fran. 402. 1897.—JEPSON has raised the var. *sparsiflora* Gray to specific rank, and it seems to us that the above variety deserves equal recognition. *E. brevifolia* has the heads in terminal clusters as in the species, but the leaves resemble those of *E. sparsiflora*. As a result, the aspect of the plant is distinctive. Furthermore, each species is confined to its own range; *E. brevifolia* grows in northern California and southwestern Oregon, and is the northernmost species of this group of curious composites.

LACTUCA SPICATA (Lam.) Hitch., var. **multifida** (Rydb.), n. comb.—*L. multifida* Rydb. Mem. N.Y. Bot. Gard. 484. 1900.—The salient character of this plant (linear or narrowly lanceolate leaf divisions) is a striking one, but except for this foliar difference the plant is referable to *L. spicata*. Accordingly, its relationship is better indicated if it is treated as a variety of that species. The variety is found throughout the Northwest, but it is not frequent.

ROCKY MOUNTAIN HERBARIUM
UNIVERSITY OF WYOMING, LARAMIE

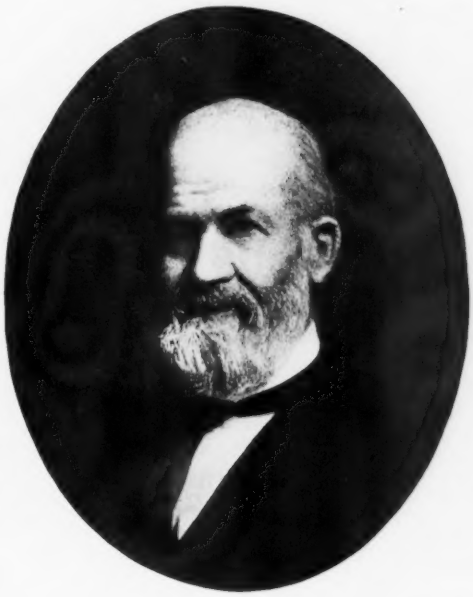
BRIEFER ARTICLES

THOMAS JONATHAN BURRILL

APRIL 25, 1839—APRIL 14, 1916

(WITH PORTRAIT)

From the moment of recognition of "the new botany," as one of them called it, three men of the middle west have stood out in prominence: BEAL in Michigan, BESSEY in Iowa and Nebraska, and BURRILL in Illinois. Each has exercised an influence on American botany further reaching than those of their generation have recognized while it was active, and each has been a force outside the field of his chosen profession.



Professor BURRILL was a microscopist, in the days when microscopy was finding itself. Only a few months ago we picked out the faces of the active workers in that near science as they appeared in a group photographed nearly half a century ago. The museum of the University of Illinois devotes one wall case to a collection of the cheap microscopes that enabled a young and poor institution to show its students the things lying beyond the range of the hand lens, and the long tube binoculars that made the smallest of living things visible to the investigator. It was thus natural that, while he knew the old botany, published a list of the higher plants of the State, and continued until his death impatient of a lessening ability

in others to know them as he knew them, Professor BURRILL should have turned for his own productive work from these conspicuous beings to the smaller ones that grow as parasites on them. He has passed into the history of science as the discoverer, in the fire blight of fruit trees, that plant diseases, like animal diseases, may sometimes be caused by bacteria. Though it has given place long since to a more approved method, he introduced to the science a method of demonstrating the bacteria of tuberculosis in affected tissues, and up to the day of his short final illness he was working hopefully on a large unsolved problem in applied bacteriology.

My own contact with Professor BURRILL came over 30 years ago. I was working as a beginner on the parasitic fungi of Wisconsin; he, as a master, on those of Illinois. The correspondence was very helpful to me; it may have been helpful to him. His publications, though rendered less essential today through being replaced by more comprehensive or more readily accessible works, had the intrinsic value of originality and carefulness, and, as has been said by a friend since his death, one felt that he was writing on a subject of which he was a master.

It is only of late years that the University to which Professor BURRILL gave his life-energy has been stamping with its approval doctors majoring in his chosen field. To his inspiration, no doubt, the men who made pioneer mycological collections and studies in Illinois owe much: SEYMOUR, EARLE, WAITE, CLINTON, and others. A colleague has told me recently that, speaking approvingly of sabbatical year and similar provisions for study away from home, Professor BURRILL expressed his own sense of deprivation in never having been privileged to work in another man's laboratory. What he accomplished was doubly commendable because he did his work as a pioneer, breaking as well as blazing the trail to his goal.

Like most men of his type, Professor BURRILL was quite as useful outside his chosen profession as within its limits. Horticulture claimed his aid and was never refused. The "forestry" park of the University of Illinois is an enduring demonstration of his contention, long before the word ecology had been coined, that trees could be grown successfully on the prairie if the prairie sod was effectively broken up. The campus was planted by him, and he lived to see his saplings become large trees. Such a man could not escape administrative responsibilities. For most of his life he was Vice-President of the University; it was he to whom the trustees turned whenever an interregnum occurred, and his lasting affection for his chosen profession, and not their lack of appreciation of

his administrative talent, explains the fact that he remained in the chair of botany and did not stay in the executive offices.

As a teacher he was inspiring and beloved; as head of an important department, he possessed a breadth far beyond his own scientific activity; acting as regent, he won and held esteem as a man of unselfishness, fairness, and firmness. He is mourned as few men in his walk of life are mourned; the University pays him the highest tribute of respect and affection; and that the younger men of his immediate profession esteemed him as of their own and not of a by-gone day and generation is shown by a banquet in his honor given by the horticultural society of his State only a few months ago, and by his election at about the same time to the presidency of the National Society of Bacteriologists, and the chairmanship of the botanical section of the American Association for the Advancement of Science. His passing leaves a void.—WILLIAM TRELEASE, *University of Illinois, Urbana, Ill.*

CURRENT LITERATURE

BOOK REVIEWS

Temperature and life processes

KANITZ[1] has written a monograph containing a critical discussion of the effect of temperature on life processes. He has brought together the literature from the fields of physical chemistry, physiology, pharmacology, bacteriology, botany, and zoology. The reader will find 363 citations of literature. Consideration is given first to the effect of temperature upon the rate of chemical processes. It is found that in general the latter follow the Van't Hoff law, that is, the rate at ordinary temperatures is approximately doubled or trebled for each increase of 10° C. in temperature. The coefficient for 10° C. rise in temperature (Q_{10}) is then 2 to 3. The formulae of BERTHELOT, ARRHENIUS, VON ESSEN, and VAN'T HOFF are derived and the relationships discussed. From these data equations are deduced by which the value of Q_{10} may be calculated from experimental results at any two temperatures. For this purpose either one of the two following equations may be used:

$$Q_{10} = 10^{\frac{10\,(\log k_2 - \log k_1)}{t_2 - t_1}}$$

$$\text{or} \quad Q_{10} = \left(\frac{k_2}{k_1}\right)^{\frac{10}{t_2 - t_1}},$$

in which k_2 = rate observed at temperature t_2, and k_1 = rate observed at temperature t_1. While most chemical processes are in agreement with the Van't Hoff law, abnormal values of Q_{10} are found in certain types of reactions. High values of Q_{10} are common in monomolecular reactions, for example, in the inversion of cane sugar, $Q_{10} = 5$ to 6. Low values of Q_{10} are formed in heterogeneous system where two processes take part, one process slowing down the total rate, for example, when a process is conditioned by diffusion rate, $Q_{10} = 1.5$ to 1.2. In photochemical processes Q_{10}, with few exceptions, is not higher than 1.4, usually only 1.2 or even 1.0.

Many processes in living organisms show a temperature coefficient approximately that of the Van't Hoff law, within certain temperature limits. Among the plant processes for which this has been found to be the case the following may be mentioned: CO_2 assimilation (MATTHAEI) between 0° and 37° C.; respiration of seedlings (KUIJPER) between 0° and 35° C.; geotropic presentation time (RUTGERS) between 5° and 25° C.; phototropic presentation time

[1] KANITZ, ARISTIDES, Temperatur und Lebensvorgänge. 8vo. pp. ix+175. *figs. 11.* Berlin: Gebrüder Borntraeger. 1915.

(M. S. De Vries) between 5° and 25° C.; protoplasmic streaming in *Elodea* (Velton) between 2°.5 and 35° C.; permeability of plant cells and tissues (Rysselberghe) between 0° and 30° C.; intake of water by barley grains (Brown and Worley) between 3°.8 and 34°.6 C., etc. Among the processes in animals showing a Van't Hoff temperature coefficient are the following: heart beat frequency, pulsation of medusae, rhythmic muscular contraction, peristaltic movement of cat intestine, rhythm in frog stomach, breath frequency, propagation of nervous stimulus, latent time of muscle, rate of cell division in *Paramecium*, generation period of certain bacteria, pupation period, rate of oxygen consumption, etc.

Some high values of Q_{10} are found, especially in relation to life duration and coagulation effects of temperature. Thus, in life duration of sea urchin eggs, $Q_{10}=240$ to 1450; of *Tubularia crocea*, $Q_{10}=485$ to 3900; of barley grains, $Q_{10}=10$ to 16; of spores of certain bacteria, $Q_{10}=8$, 15, 30, 50, or even 320. In denaturing haemoglobin, $Q_{10}=14$; and in precipitation of egg white, $Q_{10}=635$. Some processes that give normal values of Q_{10} within a certain temperature interval show high values of Q_{10} at the lower or critical temperatures. Thus, in CO_2 assimilation, $Q_{10}=28.7$ from $-6°$ to 0° C.; in heart frequency, $Q_{10}=13.7$ from 3°.2 to 8°.4; in geotropic presentation time, $Q_{10}=20$ from 0° to 5°; in protoplasmic streaming in *Vallisneria*, $Q_{10}=14.7$ from 1°.25 to 3°.75.

Kanitz brings out more clearly the relation of temperature to life processes by recalculating Q_{10} at the various temperature intervals, instead of indicating only the average coefficient for a long temperature range. When this is done, it is found that in many cases Q_{10} is not a constant at all intervals of temperature. Many processes show falling values of Q_{10} at higher temperatures, for example, CO_2 assimilation, respiration of seedlings, permeability of plant cells, etc. Some processes, however, show a temperature interval at which Q_{10} is constant. In general, in plants the range of temperature within which Q_{10} may be constant begins at 5° C. and ends at approximately 25° C. The rapidity of division of *B. coli* shows two temperature regions with constant coefficients, but with different coefficient values. Investigators should follow Kanitz in this regard, and should calculate Q_{10} for each temperature interval for which data are available.—F. E. Denny.

Heredity and environment

One of the notable recent books in the general field of genetics is that of Conklin,[2] which is a series of lectures delivered at Northwestern University on the "Norman W. Harris Foundation." The author has been unusually successful in maintaining a clear and popular style without any appreciable sacrifice of scientific values. The book departs from the usual type of textbook in genetics in several respects. In the first place, great emphasis is placed

[2] Conklin, E. G., Heredity and environment in the development of men. 8vo. pp. xiv+533. Princeton University Press. 1915.

upon the environmental and functional factors of development as opposed to the heredity factors proper. In his zeal to point out the fact that geneticists have neglected the environmental factors, the author tends to overemphasize its relative value in development and heredity. Again, his point of view conflicts with the usual genetical conception of the physical basis of heredity in that he strongly emphasizes the cytoplasmic as opposed to the nuclear elements in germ cells. He points out "that at the time of fertilization the hereditary potencies of the two germ cells are not equal, all the early stages of development, including the polarity symmetry, type of cleavage, and pattern or relative positions of future organs, being foreshadowed *in the cytoplasm of the egg cell*, while only the differentiations of later development are influenced by the sperm. In short, the egg cytoplasm fixes the general type of development and the sperm and egg nuclei supply only the details." Has the author intended to deny to the sperm a cytoplasmic organization, which might conceivably have something to do with development and heredity?

Another distinctive feature of the book is the humanistic point of view that is maintained throughout. As the title indicates, *man* is the center of interest, and the author views man broadly, neglecting none of his salient qualities. Not only is the physical development and heredity of man discussed, but a similar attempt is made to correlate with the physical side that side which we usually term the mental and spiritual. With some boldness the author, in his final chapter entitled "Genetics and ethics," invades ground that even angels might fear to tread. Such questions as "the voluntaristic conception of nature and of human responsibility," "the determinism of environment," and "responsibility and will" are handled with confidence, and certain conclusions are reached and stated, in spite of our lack of a factual and experimental basis for any such conclusions.

The 6 chapters of the book may be characterized as follows. "Facts and factors of development" includes a discussion (1) of the phenomena of development of body and of mind, and (2) of the factors of development (preformation and epigenesis, heredity and environment). The second chapter, entitled "The cellular basis of heredity and development," and the first, previously cited, are decidedly the best in the book, as might be expected in view of the author's special attainments in this field. The reviewer knows no better treatment of these important matters, although he is unable to agree with some of the author's most fundamental positions. The third chapter, "The phenomena of inheritance," is a clear, though brief, statement of the facts, observation, statistical, and experimental, that make up the body of our modern knowledge of heredity. In the fourth chapter, entitled "Influence of environment," the author has an axe to grind and does it with thoroughness. Environment and functional activity as factors in development are given a place as important as heredity. While possibly somewhat overstated, this position is one that needs to be borne in mind, and this chapter will go far toward reinstating the factors of environment and functioning in the estimation of the student of

development and heredity. The fifth chapter, dealing with the "Control of heredity: eugenics," is a somewhat conventional treatment of an important subject. The sixth chapter, entitled "Genetics and ethics," has been commented upon previously.

A useful bibliography, glossary, and index complete the volume, which, though possibly not so well adapted as some for textbook use, is, in the reviewer's opinion, probably the best presentation of genetics for the non-scientific reader.—H. H. NEWMAN.

Bacteria and plant diseases

The third volume of SMITH'S[3] *Bacteria in relation to plant diseases* continues the treatment of the vascular diseases which was begun in the second volume with a discussion of the wilt of cucurbits, the black rot of crucifers, and the yellow disease of hyacinths. In the present volume a full treatment is accorded Cobb's disease of sugar cane, Stewart's disease of sweet corn, the Grand Rapids tomato disease, the brown rot of the Solanaceae, and the wilt diseases of tobacco. These diseases have been extensively investigated by the author himself. The accounts, therefore, contain not only a complete and critical discussion of the literature, but also embody the author's own results and present his viewpoint at the time of the writing.

In addition to these diseases, to which the greater part of the volume is devoted, a number of diseases of minor importance, or such as have not been seen by the author, or whose right to be classed as bacterial diseases has not been definitely established, are considered. Among these may be mentioned several diseases of the sugar cane, some of which are probably identical with Cobb's disease, a disease of amaranths, a wilt of the peanut, a disease of orchard grass, various vascular diseases of the banana, and two diseases of the potato. The status of many of these is still obscure. That some of them, as the various diseases of the sugar cane and the many wilts of tobacco and other solanaceous plants, are not all distinct is the belief of the author, but, in accordance with his custom, each disease independently described is kept separate until its identity shall have been established.

The book may well be said to be a record of the present status of our knowledge of the diseases of which it treats. At the same time it bears internal evidence in the many changes during the making that this status is rapidly shifting. By bringing together and classifying the vast mass of scattered and fragmentary facts relating to the subject, the author has laid bare the gaps in our knowledge and has thus pointed the way for further research. Many gaps have been filled by the author's own work, but that much remains to be done before even the morphological and etiological phases of the subject shall have been cleared up is shown by a glance through the chapters on the brown

[3] SMITH, ERWIN F., Bacteria in relation to plant diseases. Vol. III. pp. viii+309. *pls. 47. figs. 138.* Washington, D.C. 1914.

rots of the Solanaceae and on the tobacco wilts with their confusion of diseases described from different parts of the world and attributed to various organisms. It is the great merit of the author to have contributed so largely to the field of plant bacteriology. It is an almost equal merit to have clearly pointed out the lines for future progress.—H. HASSELBRING.

MINOR NOTICES

A popular guide to mosses.—Mrs. DUNHAM[4] has undertaken to present the mosses of the northeastern states in a non-technical way, so that the amateur may recognize at least their genera without using even a hand lens. The result is a very attractive little book, whose simple language and marginal illustrations should accomplish the purpose announced. If it succeeds, it will open up to the general student a group of plants present in every flora, and usually regarded as too difficult for even a speaking acquaintance.—J. M. C.

Plant diseases.—A second edition of MASSEE'S[5] very useful manual has just appeared, 5 years after the publication of the first edition. It differs from the former edition only in containing a supplement of 16 pages, giving statements concerning 20 diseases which are not included in the body of the text, or concerning which additional information is given.—J. M. C.

NOTES FOR STUDENTS

Evolution of species in Ceylon.—WILLIS[6] has followed his recent paper on the endemic flora of Ceylon[7] by developing still further his argument against natural selection as an explanation of the geographical distribution of species. His argument is based mainly upon statistics derived from TRIMEN'S *Flora of Ceylon*, in which the species are divided into 6 classes, ranging from "very common" to "very rare." He observes that in Ceylon the endemic species are the rarest, according to the foregoing classification, while species which are widespread outside of Ceylon are commonest there also. This not only appears from a consideration of the flora as a whole, but in every family the endemic species are the rarest. It also appears that within every family the groups of species into the rarity classes are remarkably alike. WILLIS regards these phenomena as the result of some natural cause working with practically even pressure throughout the whole plant kingdom, a cause entirely unlike natural selection, which is essentially differentiating in its results. This

[4] DUNHAM, ELIZABETH MARIE, How to know the mosses; a popular guide to the mosses of the northeastern United States. 8vo. pp. xxv+287. Boston: Houghton Mifflin Co. 1916. $1.25.

[5] MASSEE, GEORGE, Diseases of cultivated plants and trees. 8vo. pp. xii+602. *figs. 173*. New York: Macmillan. 1915.

[6] WILLIS, J. C., The evolution of species in Ceylon, with reference to the dying out of species. Ann. Botany **30**:1–23. 1916.

[7] BOT. GAZ. **61**:82. 1916.

cause he claims is age, not the absolute age of a species, but its age in the locality. Thus endemic species are rare because they are "in the earlier stages of spreading."

WILLIS treats the two main objections to his theory as follows. The claim that the endemic species are really the oldest he answers with the evidence that frequently endemic species belong to widespread genera. These genera could not have originated in Ceylon; the endemic species must have arrived there late in the history of the genera in question. The other objection, which is merely the claim for natural selection, is that local species develop in response to local needs or conditions; but WILLIS finds that endemic species of a given rarity spread over an area of given diameter, although it may contain other kinds of soils, climates, and floras. Also the geographical boundaries of various endemic species do not coincide; that is, the species do not occupy jointly areas where special local conditions may exist. The arithmetical regularity of distribution of species within the various "rarity classes," and the geometrical regularity of the species boundaries, irrespective of physiographic or meteorologic conditions, must be explained by the mechanical, undifferentiating result of age.

In accordance with this theory, the figures given by WILLIS show that parasites, saprophytes, and climbers are "rarer" than independent plants, as should be expected, for they must have followed the others historically. It also appears that among water plants the dicotyledons are more common (therefore older) than the monocotyledons. Of angiosperms in general, WILLIS found no species that was "dying out." He believes that species die out only by accident, a more extensive accident being necessary for the disappearance of a "common" species than for a "rare one."—MERLE C. COULTER.

Securing complete germinations.—A difficulty often encountered by the geneticist is the failure of many seeds to germinate with desirable promptness. It is well known that in certain species of *Oenothera*, half or more of the seed-like structures contain no embryos, and that in many cases those seeds which do contain embryos are subject to delay in germination. DE VRIES[8] has found that in many cases he can more than double the number of prompt germinations by soaking the seeds for 2 days in water and then subjecting them submerged in water for 24 hours in an autoclave to a pressure of 6–8 atmospheres. The author assumes that the effect is due to the forcing of the water needed for germination through minute rifts in the hard portion of the seed coats. He gives a number of instances to show the contrast between seeds merely soaked, and those which have been subjected to pressure. In certain cases he found it advantageous to subject the seeds a second time to pressure. A very small percentage of the seeds resisted this treatment.

[8] DE VRIES, H., Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck. Biol. Centralbl. **35**:161–176. 1915.

DAVIS[9] has also devised a method for increasing the rapidity and total percentage of germination in *Oenothera* seeds. He places the seeds on pads of filter paper in Petri dishes, adding water until a surplus remains about the edge of the pad. The dishes, covers, papers, and water are all sterilized before the seeds are inserted. The dishes, covered and kept in shaded portions of the greenhouse, showed much more prompt and complete germinations than samples of the same seeds sown in soil. The author notes that after periods of high temperature there followed a burst of germinations, and believes that the best results will be secured by subjecting the dishes of seeds to high temperatures in an incubator. DAVIS points out as one of the distinct advantages of his method that all seedlike structures which fail to germinate remain available for subsequent study.—GEO. H. SHULL.

Color inheritance in Oxalis.—Several wild forms of *Oxalis* growing in nature at Tokyo, Japan, are found by NOHARA[10] to constitute true breeding biotypes, and one wild form indicated its hybrid nature by producing 3 types of offspring in approximately a 1:2:1 ratio. The 4 homozygous biotypes were subjected to genetical analysis by controlled breeding. Reciprocal and double reciprocal combinations yielded only the same results as the single crosses, showing no differential effect of maternal and paternal germ cells. The 4 forms differed from each other in the presence and absence of a purple bar across the base of the petals forming an "eye," and in the occurrence of several degrees of purple coloration in the leaves. The leaf and flower pigmentation are associated, either by linkage or by the production of purple color in the leaves and the purple eye spot in the flowers by the same gene. As one of the true breeding forms has purple leaves and no eye spot, the relation of these characteristics seems to be more logically referable to linkage. The 4 forms differ from one another severally by single factors, thus presenting an instance of BAUR'S "triangle," or multiple allelomorphism, athough the significance of this fact does not seem to have been appreciated by the author. In all crosses the heterozygotes are intermediate between the parents, the F_2 showing ratios approximating 1:2:1, and the F_3 behaviors are typical of Mendelian monohybrids. Three of NOHARA'S forms are recognized by him as the taxonomic forms *O. corniculata* L., *O. stricta* L., and *O. corniculata tropaeoloides* (Schlachter) Makino, and the importance of such genetical studies in the solution of taxonomic problems is made clear.—GEO. H. SHULL.

Relation of leaves to climate.—BAILEY and SINNOTT,[11] in continuing their study of the phylogeny of angiosperms, have begun an investigation of the

[9] DAVIS, B. M., A method of obtaining complete germination of seeds in *Oenothera*, and of recording the residue of sterile seedlike structures. Proc. Nat. Acad. Sci. 1:360–363. 1915.

[10] NOHARA, S., Genetical studies on *Oxalis*. Jour. Coll. Agric. Imp. Univ. Tokyo 6:165–182. *pl. 1.* 1915.

[11] BAILEY, I. W., and SINNOTT, E. W., The climatic distribution of certain types of angiosperm leaves. Amer. Jour. Bot. 3:24–39. 1916.

distribution of various types of leaves in the principal phytogeographic regions, having in view "the question of the conservatism of foliar characters and their modification by environmental factors." The present paper summarizes the results from data obtained in reference to the distribution of entire and non-entire leaves and leaflets of dicotyledons. The authors conclude that there is a marked correlation between leaf margin and environment in the distribution of dicotyledons. Entire margins predominate in lowland tropical regions; while non-entire margins predominate in mesophytic cold-temperate regions. In the tropics non-entire margins are favored by "moist uplands, equitable environments, and protected, comparatively cool habitats." In the cold temperates, entire margins are favored by "arid environments and other physiologically dry habitats." These correlations are exhibited more strikingly by trees and large shrubs than by herbs. If these conclusions are tenable, "the determination of the percentages of the entire and non-entire leaves in Cretaceous and Tertiary dicotyledonous floras affords a simple and rapid means of gauging the general climatic conditions." Attention is called to the danger of inferring that leaves are conservative or inconstant because in some cases they remain unaltered through long periods, and in other cases they vary greatly among closely related forms. A very definite relation between the evolution of climate and the evolution of plants is becoming increasingly evident.—J. M. C.

Embryo sac of Onagraceae.—The embryo sac of this family, the subject of a good many investigations, has been reported as persistently 4-nucleate, with an occasional more or less doubtful exception. TÄCKHOLM[12] has investigated the situation and confirms the constancy of this feature, stating that he never observed an embryo sac that was not 4-nucleate, nor did he find any transition stages to the ordinary 8-nucleate type. Previous statements in reference to vanishing antipodals, thus reducing the number of nuclei to 4, are thought to be accounted for by confusing them with the remnants of the 3 lower megaspores, the uppermost megaspore in this family developing the embryo sac. In fact, it seems that one or more of the 3 lower megaspores often persist attached to the embryo sac, and this sometimes results in a striking resemblance to 3 antipodals in a linear series. This union of persistent megaspores with the embryo sac constitutes what TÄCKHOLM calls a gametophytic entity, sometimes intervening walls disappearing and the persistent megaspore nuclei left free in the antipodal region of the sac. As to the possible nutritive function of these persistent and occasionally proliferating megaspore nuclei, there has been much discussion, but no certain evidence. In any event, this behavior of the Onagraceae seems to be unique, and its possible phylogenetic significance must be left at present to the imagination.—J. M. C.

[12] TÄCKHOLM, GUNNAR, Beobachtungen über die Samenentwicklung einiger Onagraceen. Svensk. Bot. Tidsk. **9**:294–361. *figs. 16.* 1915.

History of gymnosperms.—BERRY[13] has published his paper prepared for the symposium on gymnosperms at the meeting of the Botanical Society at the University of California last August. He outlines the paleobotanical evidence in reference to gymnosperms, which extends more or less continuously from the Devonian to the present time. A diagram not only summarizes the data as to the age and relative abundance of the groups, but also indicates the author's suggestions as to phylogeny. The cycadophyte phylum rises directly from the fern stock through Cycadofilicales, which group in turn gives rise to Williamsoniales, Cycadeoidales, and Cycadales. This splitting up of Bennettitales into two phyla seems to be justified by our increasing knowledge of the *Williamsonia* forms. The Cordaitales are represented as having an independent origin from the fern stock and developing the coniferophytes. The araucarians are credited with being the oldest conifer stock, the groups of Pinaceae being left in a more or less problematical position as to age of origin and ancestral group, and among them the Abietineae are regarded as more modern than the Taxodineae and Cupressineae. Taxaceae and the Ginkgoales are left unconnected, the latter beginning in the later Paleozoic, and the former recognized at the base of the Mesozoic.—J. M. C.

Morphology of Phylloglossum.—SAMPSON[14] has investigated this much discussed monotypic genus, chiefly with reference to its "annual storage tuber," the so-called "protocorm" of TREUB. As a result of detailed anatomical investigation, the author concludes that this tuber is "a specialized leafy axis, the terminal bud of which functions both as a means of vegetative reproduction and as an organ of perennation," comparable with the resting buds of *Lycopodium inundatum* and the "tubers" of certain Indian species of *Selaginella*. That in fertile plants the tuber is a modified branch is supported by the following facts: (1) a gap is left in the stele of the main axis by the exit of the vascular strand of the tuber; (2) the stele of the tuber often shows a corresponding gap; and (3) the tuber bears leaves, some of which are considerably reduced. The sterile plant consists of a simple axis, the apex of which has formed a storage tuber. The author concludes that the tuber of *Phylloglossum*, therefore, can no longer be compared with the protocorm of *Lycopodium cernuum*, but the two genera are found to be more nearly related by the fact that *Phylloglossum* is shown to be not characteristically an unbranched form.—J. M. C.

Flavone derivatives in plants.—SHIBATA and KISHIDA[15] find that aerial parts of high mountain plants are generally much richer in flavone bodies

[13] BERRY, E. W., The geological history of gymnosperms. Plant World **19**:27–41. *figs.*, 2. 1915.

[14] SAMPSON, K., The morphology of *Phylloglossum Drummondii* Kunze. Ann. Botany **30**:315–331. *figs.* 5. 1916.

[15] SHIBATA, K., und KISHIDA, M., Untersuchungen über das Vorkommen und physiologische Bedeutung der Flavorderivate in den Pflanzen. II Mitt. Bot Mag. Tokyo **29**:316–332. 1915.

(yellow pigments of the cell sap) than are plants grown on the plains. They believe that these pigments protect the mountain plants against the high insolation (especially actinic rays) of their habitat. Contrary to KERNER, they believe that anthocyanin in the foliage of mountain plants has little protective significance against light, for it develops mainly in the autumn after the light intensity has fallen. They consider the anthocyanin in foliage organs as originating by the reduction of the flavone bodies and thereby offering a problem in cell physiology, rather than being of physiological significance. They do not deny that anthocyanins of the brilliantly colored mountain flowers are of significance as light screens. They also emphasize the protective function of flavone bodies in the white and yellow flowers. The mountain plants show a great reduction in flavone content when they are grown on the plains. For a general statement of the chemical side of this problem the reader is referred to a recent review upon anthocyanins.[16]—WILLIAM CROCKER.

Morphology of Isoetes japonica.—WEST and TAKEDA[17] have investigated this species, rather widely distributed in Japan, and the largest species of the genus known, the stem ("caudex" of the authors) of an old plant often attaining 4 cm. in diameter, and in very large specimens a diameter of 8 cm. may be reached. The trilobed caudex consists of two distinct structures, stem and rhizophore, to which the leaves and roots are attached respectively, but on account of the stunted growth all external morphological differentiation between the two organs is lost. The stem apex is a conical mass of tissue at the base of the funnel-shaped depression in the cortex, and in this protuberance no apical cell can be distinguished. The primary vascular axis is "a non-medullated monostele," and no secondary xylem is formed in this species. The rhizophore, a distinct root-bearing organ, is regarded in *Isoetes* "as an organ *sui generis*." The anatomy of stem, rhizophore, and leaf is described in detail. The authors conclude that *Isoetes* "occupies an isolated position amongst recent vascular cryptogams, and is regarded as the sole living representative of the class Isoetales."—J. M. C.

Permeability.—FITTING[18] finds the plasmolytic method rather serviceable for studying the intake of salts by the cells of various plants, especially *Rhoeo discolor*, which was used mainly in the investigation. Permeability to salts of alkali metals (K, Na, and Li) is rather great. It varies with the leaf and is greatest in summer and very slight in winter. The permeability for sodium and potassium salts was about equal and for the lithium salts considerably lower. The permeability was largely determined by the anion, the sulphate

[16] BOT GAZ. **61**:349–352. 1916.

[17] WEST, CYRIL, and TAKEDA, H., On *Isoetes japonica* A.Br. Trans. Linn. Soc. London **8**:333–376. *pls. 23–40. figs. 20.* 1915.

[18] FITTING, HANS, Untersuchungen über die Aufnahme von Salzen in lebende Zelle. Jahrb. Wiss. Bot. **56**:1–64. 1915.

entering less readily than the nitrate or the chloride. It is of great interest that a considerable sojourn in a hypotonic solution lowered the permeability of the cell to the salt and apparently to the water. FITTING says that this is not a toxic effect. The method shows no evidence that the salts of metals of alkaline earths (Mg, Ca, Ba, and Sr) enter the cells, so equilibrium between the inside and outside need not be reached even in a solution of an essential salt. One wonders whether the permeability in a plasmolytic concentration throws much light on permeability in natural conditions.—WILLIAM CROCKER.

Morphology of Peranema.—DAVIE[19] has investigated the development of the sorus, sporangium, and gametophyte of this Indian fern. The study was suggested by the possible intermediate character of the genus between Cyatheaceae and Polypodiaceae. The receptacle is of the Gradatae type, but the mature sorus is a mixed one. The sporangium also in its early segmentation sometimes follows the type of one family, and sometimes that of the other family. In comparing the features of the genus, the conclusion is reached that an intermediate series consisting of *Woodsia*, *Diacalpe*, and *Peranema* is probable, *Woodsia* coming nearest Cyatheaceae, and *Peranema* nearest Polypodiaceae. The mature sorus of *Peranema* is thought to be most related to that of *Nephrodium*, and a phyletic line is traced from the Cyatheaceae to the Aspidieae group of the Polypodiaceae.—J. M. C.

Two new terms.—TRELEASE[20] has proposed two new botanical terms to be applied to hitherto nameless morphological conditions. He points out that the old grouping of plants into thallophytes and cormophytes fails to include such plants as mosses, which are not cormophytes because, although "stem-like," they do not develop root and shoot. He proposes, therefore, a grouping of plants into 3 categories: thallophytes, "cormophytasters" (or pseudo-cormophytes), and cormophytes. The second term, "xeniophyte," is proposed for the so-called endosperm of angiosperms, which being neither an x nor a $2x$ generation is a third generation which has been "overlooked." The angiosperms, therefore, in addition to their other peculiar features, are unique in having 3 generations: sporophyte, gametophyte, and xeniophyte.—J. M. C.

Seed germination in Megarrhiza.—HILL[21] has investigated the peculiar seed germination of several species of this genus, which is also known as *Marah*. The petioles of the cotyledons are "fused together" to form a tube, which

[19] DAVIE, R. C., The development of the sorus and sporangium and the prothallus of *Peranema cyathoides* D. Don. Ann. Botany **30**:101–110. *pl. 3. figs. 2.* 1916.

[20] TRELEASE, WILLIAM, Two new terms, cormophytaster and xeniophyte, axiomatically fundamental in botany. Proc. Amer. Phil. Soc. **55**: 237–242. 1916.

[21] HILL, A. W., Studies in seed germination. The genus *Marah* (*Megarrhiza*), Cucurbitaceae. Ann. Botany **30**:215–222. *pl. 5. figs. 2.* 1916.

grows out of the seed carrying the plumule and hypocotyl with it. The length of the tube varies in different species, and in *M. horridus* the elongated tube bears "absorbent hairs." In emerging from the tube the hypocotyl breaks through at the base, and later the plumule pierces the side of the tube. Eventually a hypocotyledonary tuber is formed, which may become very large. In *M. horridus* the interesting discovery was made that in connection with the growth of this tuber the cotyledonary tube splits into 6 separate parts, each of which contains a vascular strand.—J. M. C.

An automatic transpiration scale.—The extensive work of BRIGGS and SHANTZ[22] upon the water relations of plants in arid and semi-arid regions, and more particularly their water requirement measurements, has necessitated the construction and use of an automatic scale of 200 kg. capacity, sensitive to 5 gm., in order to measure the transpiration of plants freely exposed to wind and weather. Such a scale is described in a recent publication.[23] In it steel balls are used as weights, and continuous records for periods of several weeks are obtained. The article also contains a review of other forms of transpiration balances, both of the step-by-step type, which includes the scale here described, and of the continuous record type.—GEO. D. FULLER.

Field rot of potato tubers.—PRATT[24] points out some interesting facts that he discovered in his studies of the potato rot situation in Idaho. "Stem end rot," "field rot," or "black rot" of potatoes of the round type, such as Rurals and Pearls, and jelly end rot of tubers of the Burbank group are induced by *Fusarium radicicola*. The organism is active at temperatures above 50° C. and can therefore be controlled in storage. Field control of the black rot situation is difficult. Seed pieces afflicted with black rot bring about infection of the following potato crop, and, interestingly enough, virgin soils produce heavier infection than lands that have been put to crops.—G. K. K. LINK.

Recent work in embryology.—SOUÈGES,[25] in continuing his embryological studies, has published an account of the Cruciferae, which traverses the classic work of HANSTEIN and FAMINTZIN. The figures are chiefly those of *Lepidium sativum*, although other species of *Lepidium* (*L. campestre* and *L. Draba*) and *Cochlearia officinalis* are included.

[22] BOT. GAZ. **56**:514–515. 1913.

[23] BRIGGS, L. J., and SHANTZ, H. L., An automatic transpiration scale of large capacity for use with freely exposed plants. Jour. Agric. Research **5**:117–132. *pls. 9–11. figs. 18.* 1915.

[24] PRATT, O. A., A western field rot of the Irish potato tuber caused by *Fusarium radicicola*. Jour. Agric. Research, Dept. Agric. **6**:297–309. *pls. 34–37.* 1916.

[25] SOUÈGES, M. R., Développement de l'embryon chez les Crucifères. Ann. Sci. Nat. Bot. **19**:311–330. *pls. 11–14. figs. 76.* 1914.

CARANO has published the results of the investigation of the development of the embryo in Asteraceae,[26] *Senecio vulgaris*,[27] and *Poinsettia pulcherrima*.[28]—J. M. C.

Water absorption by epiphytes.—LIESKE,[29] studying certain epiphytes (*Epidendrum* and *Tillandsia*) in their natural habitats about Rio de Janiero, concludes that the velamen of the former and the scales of the latter do not condense physiologically significant amounts of water from the air. The water needs are supplied by rain, dew, and mist. The scales of *Tillandsia* seem important in trapping salts as dust from the air, which are later dissolved and absorbed.—WILLIAM CROCKER.

Toxicity of lithium salts.—FERKING[30] obtains some interesting results upon the toxicity of lithium salts. He finds that lithium salts, like magnesium salts, are highly toxic only to calcium-requiring plants and not injurious to the lower algae (*Chlorella* and *Scenedesmus*) and fungi (*Penicillium glaucum*) that do not require calcium. While calcium salts can fully antagonize the injurious effects of magnesium salts, they only reduce the toxicity of lithium salts.—WILLIAM CROCKER.

Morphology of Pittosporum.—BREMER[31] has investigated the ovule and embryo sac of two species of *Pittosporum*, and reports that in both cases the nucellus degenerates and has disappeared when the embryo sac is mature. In *P. ramiflorum* the third megaspore of the linear tetrad develops the embryo sac; and in *P. timorense* the tetrad is bilateral instead of linear.—J. M. C.

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[29] LIESKE, R., Beiträge zur Kenntnis der Ernährungsphysiologie extrem atmosphärischer Epiphyten. Jahrb. Wiss. Bot. **56**:112–122. 1915. PFEFFER'S Festschrift.

[30] FERKING, H., Über die Giftwirkung Lithiumsalze auf Pflanzen. Flora **108**: 449–453. 1915.

[31] BREMER, G., Reliquiae Treubianae II. The development of the ovule and embryo sac of *Pittosporum ramiflorum* Zoll. and *Pittosporum timorense* Blume. Ann. Jard. Bot. Buitenzorg II. **14**:161–164. *pls. 23–26*. 1915.